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OF

HUMAN AND COMPARATIVE

HISTOLOGY.

EDITED BY

S. STRICKER.

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VOLUME III.

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PREFACE.

BY PROFESSOR STRICKER.

THE Science of Histology rests on more numerous and more exact observations than any other department of knowledge. The microscope effects the enlargement of the image falling upon the retina, and by thus diminishing the extent of surface that can be examined at once, we gain proportionately in sharpness.

Constant practice enables us to raise the acuteness of our perception of luminous rays to an extraordinary degree. We place ourselves in a convenient position; we put away from us all extraneous disturbing impressions on our senses, and even concentrate the sensation of light upon one eye. Nay, more, we even endeavour to save this organ every secondary or subsidiary effort, neither permitting it to roll nor allowing any accommodation to be effected. We take, so to speak, the eyeball into our very hands, we accommodate it by a screw, and turn it about by means of a mechanical stage.

Our region of observation, thanks to the improvements in the microscope, has not only waxed in breadth during the last ten years, it has also gained in depth and clearness through the distribution of the "lights" of careful observation. In yet another direction, too, is our sphere being enlarged. Histology is constantly and steadily advancing to the dignity of a comparative Science. Each worker conse-

quently finds it more and more difficult to acquire such a grasp of the whole subject as is requisite to enable him to give a scientific description of it.

It was with feelings of this kind that I undertook the Editorship of the present collection; and the willing co-operation I have obtained from the best workers of the day, on the one hand, and the liberality of the publishers on the other, have enabled me to bring it to a happy conclusion.

A review of the whole work, however, compels me to admit that it does not present the same uniformity that it would otherwise have done had it been the outcome of a single master mind. Some pages glow with the results of the long-continued industry of the best investigators of our time, and sometimes again these nodal points, so to speak, appear joined together by the labour of younger hands. It lacks, however, that whitewash with which our master builders, following the usual custom, are wont to cover their constructions in order to hide from the eye of the observer all the piece-work of their men—the good bits equally with the bad.

My collaborateurs will, however, suffer no detriment by aiding in the construction of this fabric, how rude soever it may be. The more experienced and advanced certainly not, for light is never darkened by a less light, whilst the younger ones will assuredly not complain that their participation is manifest.

It can only then remain a question whether the reader, and above all, whether Science, has gained anything by this proceeding. The two questions are really reducible to one; for the interests of the reader cannot be better promoted than by presenting to him whatever best responds to the demands of the advance of Science.

It requires no further argument to prove that the true features are better seen in proportion as the use of paint is avoided.

It cannot be denied that in the composition of Manuals on Histology the colour-top still plays a prominent rôle; our knowledge of this subject is still of the nature of a mosaic, and in the exposition of the whole we eagerly cover the mosaic with our paint. This is no doubt perceptible, to some extent, even in this work; but it is less apparent in proportion as the several chapters approximate the characters of monographs; it is moreover all the less injurious, inasmuch as the whole is not pervaded by any one style. On the contrary, the many and various modes of treatment observable in our work form not the least of its excellencies. It thereby comes nearer that goal towards which all handbooks should strive; viz., to draw a picture of the condition of theories at a given period. Such a picture will the more closely approximate truth the more completely the predominance of each individual is suppressed.

The variety of the mode of treatment nevertheless has an attendant evil. The various co-workers are opposed to one another in questions that are not altogether unessential. This evil will however only trouble those who place the convenient arrangement of their knowledge higher than truth. The learned, and those who would become such, will, I feel sure, be satisfied that I have given space to conflicting views. "Durch den Widerspruch wird der Geist der Prüfung genährt." (Controversy is the mother of inquiry.)

S. STRICKER.

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CHAPTER XXXIII.

THE ORGANS OF TASTE.

By Th. W. ENGELMANN,

OF UTRECHT.

a. Organs of taste of Man and Mammals.

For some time past physiologists have recognized the principal regions in Man in which the peripheric terminal apparatus of the gustatory nerves must be situated, and have concluded that they are represented by the superior surface of the root of the tongue (especially the papillæ circumvallatæ), the borders and apex of the tongue, and probably also the anterior portion of the soft palate. Observations and experiments have rendered it also probable that various kinds of terminal apparatus exist; and that these are not equably distributed over the gustatory regions. In accordance with this, microscopic anatomy has recently made us acquainted with special organs in Mammals which must be regarded as the terminal apparatus of the gustatory nerves. Chr. Lovén and G. Schwalbe, independently of each other, discovered in the laminated pavement epithelium which covers the papillæ circumvallatæ of the Mammalian tongue, numerous microscopic bud-like cell groups, which form the terminations of the branches of the nervus glossopharyngeus, named by Lovén gustatory bulbs (Geschmacks knospen and Geschmackszwiebeln), and by Schwalbe, gustatory cups (Schmeckbecher).

These organs have already been demonstrated in Man, the Dog,

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Cat, Ox, Sheep, Roedeer, Horse, Pig, Hare, Rabbit, Guineapig, Rat, and Mouse.

The gustatory bulbs (fig. 269) occupy cavities in the lingual mucous membrane, which they completely fill. As a general rule, the form of the spaces is that of a round-bellied flask (Bulb). The bottom of the flask rests upon the surface of the fibrous layer of the membrana mucosa; the slender and for the most part short neck of the flask perforates the corneal lamina of the epithelium, and opens on the surface with a circular opening, which may be termed the *gustatory pore.* The length

Fig. 269.

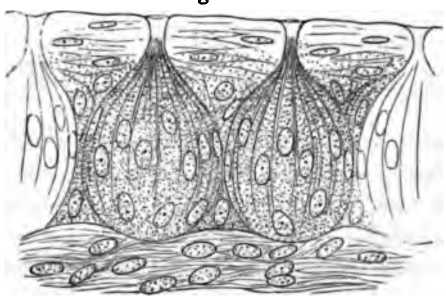

Fig. 269. Gustatory bulbs from the lateral gustatory organ of the Rabbit. Magnified 450 diameters.

of the bulb, which constantly exceeds its greatest breadth, amounts in Man to 0·077—0·081 of a millimeter; the greatest breadth is about 0·0396 of a millimeter; the width of the gustatory pore is from 0·0027 to 0·0045 of a millimeter (Schwalbe).

The gustatory bulbs present somewhat diverse forms in different animals. In some, as the Ox and Pig, they are slender and quite three times as long as broad; whilst in others, as in the Rabbit and Roedeer, they are compressed and but little longer than broad. The most slender are usually the largest. Their size likewise varies, and is not constant in the same species or even in the same individual. In many instances larger and smaller bulbs are arranged in juxtaposition, apparently without any regularity. Subjoined are a few measurements taken for the most part from Schwalbe:

	DOG.	OX.	PIG.	RABBIT.
Length of the bulbs in millimeters . . .	0·072	0·172	0·055—0·130	0·045—0·070
Greatest breadth of the bulbs in millimeters .	0·0306	0·048	0·020—0·052	0·03—0·045
Diameter of the gustatory pores in millimeters .	0·0045	0·002—0·009	0·0027	0·003—0·0045

The lateral portions of the papillæ circumvallatæ are pre-eminently the regions of the lingual mucous membrane where the gustatory bulbs are found. They here, numbering often many hundreds, form a broad girdle around each papilla. They are found also, though in general more sparsely distributed and isolated, upon the papillæ fungiformes. In the Hare and Rabbit, each side of the root of the tongue exhibits also a large oval elevation, divided into from ten to fourteen thin folds—the gustatory laminæ—by a corresponding number of parallel transverse grooves or fissures, which contain thousands of gustatory bulbs. Apart from the fungiform papillæ which now and then bear gustatory papillæ on their free surfaces, we find the organs in question always occupying protected portions of the lingual mucous membrane, such as furrows and the bottoms of fissures. Hence they are never seated upon the epithelium of the plateau in the papillæ circumvallatæ, but upon the lateral portions of those papillæ, and are therefore protected by the circular wall, and in like manner they never occupy the projecting portions of the laminæ in these gustatory folds of the lateral gustatory organ of the Rabbit, but are always seated upon their sides.

Structure of the gustatory papillæ and gustatory folds. The papillæ circumvallatæ.—The papillæ circumvallatæ (fig. 270), into a description of the manifold variations in form of which we shall not here enter, consist usually of a truncated conical body, composed of connective tissue which is invested by a laminated pavement epithelium. According to Lovén, "The papilla itself is beset upon its upper part with a great number of conical or more or less elongated, and sometimes forked, secondary papillæ; whilst the border of the

upper surface and the sides present low perpendicular folds, *i.e.*, folds running parallel to the axis of the papilla, with intervening furrows." He also observes "that these furrows are completely filled with epithelium, so that the surface of the papilla is everywhere perfectly smooth, and exhibits no trace of the subjacent inequalities. The epithelial layer is considerably thicker upon the upper surface and that portion of the papilla which is not protected by the circular wall, than upon the protected lateral portions; but even in the former situations it is far thinner than upon the remainder of the surface of the tongue. The epithelium is also very thin upon the external wall of the vallecula. The gustatory bulbs are situated in the thin epithelium at the sides of the papilla, and indeed there usually form a zone that extends from the bottom of the fossa upwards to about the level at which the papilla is no longer protected by the lateral wall (Schwalbe). The

Fig. 270.

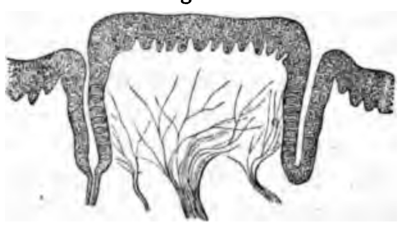

Fig. 270. Transverse section through a papilla circumvallata of a Calf. Showing the arrangement and distribution of the gustatory bulbs. Magnified 25 diameters.

zone, like the wall, entirely encircles the papilla. If the fossa be deep, as in the Sheep and Pig, the zone is broad; if, as in the Horse, it be shallow, it is narrow. In Man, however, even when the fossa is deep, the upper half of the lateral wall of the papilla appears to be destitute of gustatory bulbs (Schwalbe). The number of the gustatory bulbs is very great, since as a rule they stand in close contiguity to one another, and most so in Man, where, according to Schwalbe, they are in absolute contact. Schwalbe estimated the number present in one papilla of the Sheep, of moderate size, at 480; in one from the Ox, at 1,760; in the Pig, which only possesses two circumvallate papillæ, each has about 4,760 bulbs. This would give a total number of bulbs in the Sheep, of 9,600; in the Ox, of 35,200; in the Pig, of 9,520. In Man and in the Dog, according to Schwalbe, and in the Rat and Rabbit, according to Lovén, a few bulbs usually appear to be scattered on the outer wall of the vallecula, or that which looks towards the

papilla. The relations of the nerves found in the papillæ to the gustatory apparatus will receive consideration hereafter.

Papillæ fungiformes.—The papillæ fungiformes, between which and the papillæ circumvallatæ are many transitional forms, present also essentially similar structural characters. They, however, do not possess the mantle of gustatory bulbs. On the other hand, Lovén discovered gustatory cups in the Calf, distributed on their upper free surface, between the secondary papillæ. In the Rabbit and in the Rat he found them upon every papilla fungiformis ; though there was only one in each of the small papillæ. Schwalbe doubted at first their presence upon the fungiform papillæ, but he subsequently found them (especially in the Pig). I have also seen them in vertical sections of the papillæ in the Mouse and Cat. In Man, and in the Dog and Calf, they occur, according to Lovén, much more rarely upon the fungiform papillæ than in the animals just mentioned.

The two *lateral gustatory organs* of the Rabbit and Hare, to which allusion has just been made, appear, notwithstanding their size, to have escaped observation.* Yet they constitute gustatory organs

Fig. 271.

Fig. 271. Transverse section through a few of the gustatory lamellæ of the lateral gustatory organ of the Rabbit. Magnified 25 diameters.

of the first rank. Each consists of an oval slightly prominent elevation at the side of the root of the tongue, traversed by from ten to fourteen parallel grooves. In Rabbits, the length of the organ from before backwards is about 5—6, and in breadth from 2·5—3·5

* They are not mentioned in W. Krause's work on the anatomy of the Rabbit. They were discovered and described, independently of myself, by Hans von Wyss, "On a new Gustatory Organ in the Tongue of the Rabbit." *Centralblatt für die medizinische Wissenschaften*, 1869, No. 35, p. 548, and in more detail in the *Archiv für Mikroskopische Anatomie*, 1870. The account given by v. Wyss is in complete accordance with my own, which last, I may remark incidentally, had already been sent to press in the summer of 1869.

millimeters. In the Hare it is somewhat larger. Fig. 271 shows the appearances presented by a vertical section carried at right angles to the direction of the furrows through the middle of the organ. Here four gustatory lamellæ are seen in complete section, and two in half-section. They are separated from one another by deep grooves, at the bottom of which an acinous gland here and there opens. These folds present a body composed of connective tissue, dividing into three secondary folds, of which the centre one is broader than the two lateral. The connective-tissue matrix is invested by laminated pavement epithelium, which completely occupies the groove

Fig. 272.

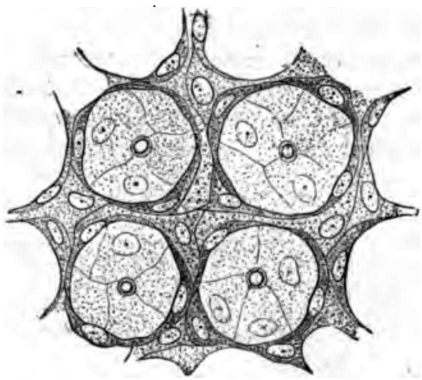

Fig. 272. Upper half of the epithelial framework of the gustatory bulbs. Four cavities, from which the bulbs have fallen out, are here seen from the side of the mucous membrane. In the centre of the bottom of each is the gustatory pore. The specimen was taken from the lateral gustatory organ of the Rabbit. Magnified 450 diameters.

between the secondary folds, and is much thicker on their free surface than laterally, where they form the boundaries of the grooves. The gustatory bulbs are placed laterally along the whole length of each lamella. They there form a broad stria, which extends downwards to about the middle of the depth of each furrow, and upwards to near the opening of the furrow. The gustatory bulbs are so closely arranged (figs. 271 and 272) as to be in absolute contact. In the Rabbit they usually stand in four tiers or ranks, one above another. Each tier may contain in its whole length about eighty bulbs. Each gustatory fold may perhaps be approximately held to contain

620 bulbs, and the two gustatory organs together (estimating them to have twelve lamellæ apiece) would thus have 14,880 gustatory bulbs.

According to the statements of Schwalbe, two similar organs are present in the Pig. They contain, however, only isolated gustatory bulbs.

As has been already stated, the gustatory bulbs (see fig. 269) occupy flask-like cavities of the epithelium, which they completely fill. The walls of these cavities, with the exception of the floor, which rests on the connective tissue of the mucous membrane, are formed by the epithelial cells themselves. At the level of the belly of the flask the epithelium is composed of cells of many different shapes, which present the characteristics of the elements of the rete Malpighii in their finely granular protoplasm, relatively large nucleus, and indistinct cell wall. The

Fig. 273.

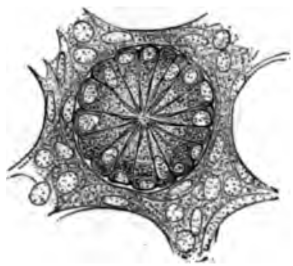

Fig. 273. A gustatory bulb exposed in consequence of the detachment of the upper half of the epithelial framework, seen from above. From the lateral gustatory organ of the Rabbit. Magnified 450 diameters.

innermost of these cells, which are cemented to the wall of the flask-like space, have a concavo-convex shape, like fragments of a watch-glass. When seen in transverse section, they are falciform (fig. 272). Around the neck of the flask and its opening, the gustatory pore, the epithelium presents the characters of the horny epithelial layer of the oral mucous membrane, the cells having a flattened form, a thick cell membrane, homogeneous contents, and flat nucleus. In those regions that are occupied by the gustatory bulbs, the horny lamina is, as a rule, only 0·01—0·02 of a millimeter in thickness, and its

inferior surface is not very sharply defined from the stratum Malpighii. The margin of the gustatory pore is generally formed by the apposition of several cells, but sometimes by a single cell, which then appears as if it were perforated by a round hole. The border of the hole often presents an annular thickening (fig. 272).

Figs. 269, 272, and 273 may serve to further elucidate this description; all three figures being taken from the gustatory lamellæ of the Rabbit. Fig. 269 shows a section carried perpendicularly through the thickness of the gustatory epithelium. The gustatory bulbs are seen occupying the flask-shaped spaces. Fig. 272 exhibits the upper half of the epithelial framework which surrounds the space for the gustatory bulbs, as seen from below. This half of the

Fig. 274.

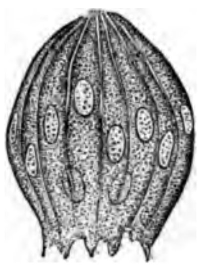

Fig. 274. Isolated gustatory bulb, from the lateral gustatory organ of the Rabbit. Magnified 600 diameters.

epithelium has raised itself as a continuous lamina from the subjacent layer in the course of the preparation of the specimen. The gustatory bulbs remain with this last seated upon the mucous membrane. The figure gives the appearances presented to the observer as seen on looking into the open and empty spaces from below; at the bottom of each may be seen the sharply defined gustatory pore, surrounded by a thickened ring. Fig. 273 completes fig. 272. It represents a gustatory bulb still attached to the mucous membrane, with the surrounding inferior half of the epithelial framework, as seen from above.

The *gustatory bulbs, or taste cups* (Geschmacksknospen oder Schmeckbecher), (fig. 274,) which occupy the above-

described spaces, consist of a number—varying, according to the size of the bulbs, from fifteen to thirty—of long, thin cells, that are arranged like the leaves of a bud. They stand in several closely compressed rows around the axis of the bud. The outermost, which are applied to the wall of the space, and are curved concentrically to it (their concavities being directed inwards), enclose those situated more internally, which are less and less curved as they approach the axis. All gustatory bulbs, it would appear, are composed of at least two principal kinds of cells; of these, one does not differ very essentially from ordinary epithelial cells, and is not in direct connection with nerves. The cells of the second kind are peculiar, highly differentiated structures, that in all probability are directly continuous with nerves, and are to be regarded as the proper *gustatory cells.* The former, which may be termed investing cells (Deckzellen), as Lovén and Schwalbe suggest, are usually the most numerous, and form the external layers of the bulb; the second appear to be chiefly situated near the axial region of the bulb.

Fig. 275.

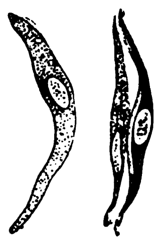

Fig. 275. Isolated investing cells, from the gustatory bulbs of the Rabbit. Magnified 600 diameters.

The *investing cells* (fig. 275) are long, rather slender, and in general somewhat fusiform structures with an ellipsoidal vesicular nucleus, which is situated either near the centre or towards one end. They consist of clear protoplasm quite free from granules. Towards the gustatory pore they gradually become attenuated to a fine point; inferiorly they either diminish but slightly, so that they still remain of considerable breadth where they come into contact with the connective-tissue surface

of the mucous membrane to which they are firmly adherent, or they gradually diminish in size, and suddenly break up into several processes that often undergo subdivision, but in many instances do not reach the surface of the membrane.

In preparations obtained from the Sheep, and treated with perosmic acid, Schwalbe found a circlet of fine short hairs at the apex of the bulb, the points of which converged towards the interior of that structure, and he was then led to the conclusion that they sprang from the apices of the investing cells. These small hairs did not undergo solution in caustic potash lye, even after long maceration, but were no longer distinctly visible after isolation of the bulbs in solutions of chromic acid. Their presence could not be distinctly demonstrated either in other animals or in Man. Investing cells, whose inferior extremities were prolonged into slender processes, were easily obtained by Lovén and Schwalbe from the gustatory bulbs of Man and of the Calf. The processes were never varicose, but often presented a capitate enlargement at their extremity. Some of the investing cells depicted by Lovén* call to mind the forked cells of the Frog, hereafter to be described; and, like these, are possibly peculiar forms of true gustatory cells. The long axis of the investing cells is usually parallel to that of the bulb, and varies within the same limits as these—in Rabbits, for example, between 0·045 and 0·065 of a millimeter. The investing cells of the same bulb are not all of equal size; but those of the outermost layer are usually the largest and widest, and at the same time the flattest. Those of the inner layer are shorter and more cylindrical.

The *gustatory cells* (fig. 276, *a* and *b*) are long and thin organs, that are always homogeneous and highly refractile. Each consists of an elliptical body prolonged at its upper pole into a moderately broad, and at its inferior pole into a slender, process. The body is formed by a vesicular nucleus surrounded by a very thin layer of homogeneous substance or "protoplasm." The superior broader (peripheric) process is in the Rabbit quite cylindrical, somewhat attenuated towards the apex, in general about two and a half to three times longer, and at its middle about half as broad, as the nucleus of the cell. The apex is usually obliquely truncated and prolonged into a short hair or cilium (fig. 276, *a*).

* *Loc. cit.*, *infra*, fig. 6, *e*, *g*, and *h*, *i*, *j*.

The apices of these hairs appear scarcely to reach in the normal state to the level of the gustatory pore. The inferior (central) process is thin, cylindrical, and even at a small distance from the nucleus is about three times more slender than the above-described peripheric process. At a distance of 0·006 to 0·0012 of a millimeter from the nucleus it usually divides into two but slightly thinner branches which extend to the surface of the mucous membrane. Before this happens, however, it divides once or several times in quick succession. The chemical relations of the central process appear to be those of a nerve fibril.

Fig. 276.

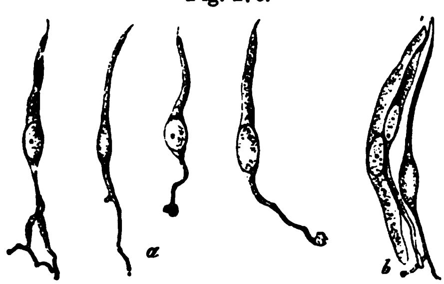

Fig. 276. *a*, Isolated gustatory cells, from the lateral organ of the Rabbit, magnified 600 diameters; *b*, an investing and two gustatory cells, isolated but still in connection with one another, from the same, magnified 600 diameters.

Lovén found that the gustatory cells of the Calf were somewhat differently constructed. In these the peripheric outrunner is cylindrical and rod-like, but supports no hair. The centric process is a long fine thread, frequently beset with various enlargements and short branches that are apparently abruptly broken off and are directed outwards. In the case of Man, Lovén found that the peripheric processes are shorter and somewhat pointed at the extremity, though in other respects they resemble those of the Calf. Schwalbe distinguished two kinds of gustatory cells in Man and the Sheep—*pin or peg cells* and *rod cells* (Stiften-zellen and Stab-zellen). In the former, which are the most common, the peripheric broader process is continuous at its attenuated extremity "with a slender highly refracting style or point, sharply truncated above." The point sometimes projects, in gustatory bulbs isolated in perosmic acid, as much as 0·0072 of a millimeter

from the apex of the bulb. The central process is filiform and sometimes varicose. Schwalbe was unable to satisfy himself of the existence of the lateral branches described by Lovén. In the "rod cells" the peripheric process is "shorter, of uniform breadth, and truncated (?) anteriorly" without the pin or pencil-like point. The central process, on the other hand, is scarcely to be distinguished from that of the ordinary gustatory cells. Whether in various regions of the tongue different forms of gustatory cells are present, which are to be regarded as the conductors of various gustatory impressions, is still unknown; and in like manner we are still ignorant whether one or several kinds of gustatory cells exist in each gustatory bulb.

THE NERVES.—We are still very imperfectly acquainted with the relations of the nerve fibres to the elements of the gustatory bulbs. We know, however, that branches of the glossopharyngeus, which chiefly consist of fine medullated fibres, are distributed to the papillæ circumvallatæ, and break up in their interior. Shortly before their entrance into the papillæ, these branches, like the trunk of the glossopharyngeus (Remak) contain small microscopic groups of ganglion cells; immediately beneath the papillæ they form a plexus which is particularly well developed in the Sheep (Schwalbe). Proceeding from this plexus, one or more large fasciculi run up in the axis of the papilla, whilst in many instances a few also penetrate its lateral surface, and then break up into numerous fine and frequently decussating sinuous branches which stream out towards the epithelium. As a general rule, these branches contain many more pale than dark-bordered fibres. The greater number of the fasciculi are usually distributed in the vicinity of the gustatory bulbs, and these expand into a thin stratum containing numerous nuclei, on which the gustatory bulbs are directly seated. According to Schwalbe, the nerves in this stratum consist, independently of the isolated medullated fibres, of fine fasciculi of fibrils, each of which is invested by a nucleated sheath, which is rendered pale and transparent by acetic acid. These fasciculi undergo continuous subdivision into smaller branches, from which at length fine pale fibres are given off, that closely resemble the processes of the gustatory cells, and form a plexus close beneath the epithelium. It is extremely probable that these finest fibrils are continuous with the central

processes of the gustatory cells. Schwalbe sometimes saw very similar fibrils project from the surface of the mucous membrane in specimens prepared in chromic acid from which the epithelium had been brushed away.

The relations of the nerves in the gustatory ridges of the Rabbit and Hare are very similar to those of the papillæ circumvallatæ. The numerous and moderately thick branches of the glossopharyngeal nerve, which ramify beneath the gustatory lamellæ, contain tolerably large, though still only microscopic, clusters of cells. In one of these I counted more than thirty cells. These were quite spherical, with an average diameter of 0·05 of a millimeter, and appeared to be in connection with a nerve at one pole only. From the larger nerve trunks, very numerous and still moderately thick fasciculi of pale fibres proceed towards the zones of the gustatory bulbs. Wherever these are situated, though not elsewhere, the mucous membrane contains numerous nuclei (fig. 271, where this character is indicated by dotting, and fig. 269). In this nucleated layer extremely numerous, very fine, pale nerve fibrils run, which agree in size, form, refractive power in regard to light, and, as it would appear, also in chemical relations, with the central processes of the gustatory cells. They may not unfrequently be followed to the base of a gustatory bulb, where they are lost.

As an appendix to the foregoing, we may here consider the descriptions given by Szabadföldy and Letzerich on the mode of termination of the gustatory nerves of Mammals. According to the former observer, they end in pyriform corpuscles that are imbedded in the connective tissue of the mucous membrane. But inasmuch as they cannot be in any case immediately touched by the substances passing through the oral cavity, whilst at the same time the gustatory sensasions are perceived much earlier than it is possible for any known solution to permeate the thick epithelial layer, it is obvious that the structures described are not gustatory organs at all, as Szabadföldy maintains. Moreover other observers have not been able to discover them. Nor have the statements of Letzerich, up to the present time, received greater support, according to whom the gustatory nerves in all the papillæ of the Cat, Ox, and Weasel terminate in "flat tolerably large vesicles, the walls of which are structureless, and beset with large nuclei. These vesicles lie upon the mucous plexus of the lingual and papillary mucous membrane." They have two kinds of processes, one of which is nipple-shaped, directed towards the connective tissue

of the mucous membrane, and connected with dark-bordered nerves that become pale fibres at the point of junction with the vesicles. The axis-cylinder traverses the nipple-shaped process, filled with protoplasm, and branches dichotomously on the internal surface of the vesicle. "Prismatic highly refractile corpuscles (terminal nerve corpuscles), closely resembling the rods of the retina, are attached to these branches. The vesicles themselves are filled by a watery, bright, granular mass." The processes of the second kind are tubular eversions of the membrane of the vesicles, extending towards the surface between the horny epithelial cells. Their ends always remain covered by a layer of epithelial cells, though this may be extremely thin. Letzerich was not able to find the gustatory organs discovered by Lovén and Schwalbe.

b. Gustatory Organs of the Amphibia.

The gustatory organs of Birds and Reptilia are still almost unknown in comparison with the far better known and long since described organs of Batrachia (Rana esculenta and temporaria, Hyla arborea). In Frogs also the terminal organs of the gustatory nerves are microscopically small clusters of peculiarly formed epithelial structures occupying spaces between the epithelial cells of the lingual and palatal mucous membrane. Their form, however, is not that of a flask or bulb, as in Mammals, but disk-like. As they completely correspond to the gustatory bulb, we shall term them *gustatory disks*. They are distributed by hundreds, and with tolerable uniformity, over the upper surfaces and borders of the tongue. Each is here supported by a broad somewhat cylindrical papilla. Numerous gustatory disks occur also in the epithelium covering the smooth non-papillated surface of the palatal mucous membrane. These do not project, or project but slightly, beyond the level of the remaining epithelium, and require further investigation.

Minute Anatomy of the Gustatory Papillæ of the Frog (Rana esculenta and temporaria).—These papillæ consist of a connective-tissue body invested by epithelium, which in general has the form of a short cylinder or truncated cone. The gustatory disk is seated upon the circular or elliptical terminal surface of this body, surrounded by a narrow girdle of ciliated

cells, and is composed of peculiar cells and cell-like bodies. The lateral surfaces of the papillæ are covered with simple non-ciliated columnar epithelium.

The connective-tissue body of the papilla consists, in its inferior and larger part, of rather loose connective tissue, in which are imbedded vascular capillary loops, muscular fibres branched at their extremities, and a fasciculus of dark-bordered nerves. The upper part is a solid disk, 0·01—0·015 of a millimeter in thickness, composed of very dense non-nucleated connective tissue, to which the name of *nerve cushion* may be applied. It forms the floor upon which the gustatory disk rests.

From five to ten dark-bordered nerve fibres enter from below into the papilla, and run in its axis almost always unbranched as far as to the inferior surface of the nerve cushion. At or just before their entrance into the latter, they become somewhat attenuated, and lose their medulla and their neurilemma. Immediately after this they divide, and appear as very fine (about 0·002 of a millimeter in diameter) and pale nerve fibres, which, after repeated dichotomous division, form a delicate and close nervous plexus which is expanded nearly horizontally in the inferior half of the nerve cushion. From this plexus, numerous fine twigs (fig. 277), again dividing, ascend in a straight or oblique direction, as far as to the surface of the nerve cushion. They here enter into connection with the elements now to be described of the gustatory disk.

The nerve fasciculi that enter the papillæ fungiformes arise from the glosso-pharyngeal nerve. The small papillæ of the Frog's tongue, which are covered with ordinary epithelium, appear, as Billroth has already stated, to be destitute of nerves. The nerve cushion, which inferiorly becomes firmly fused with the remaining connective tissue of the papillæ, but presents externally a sharp and smooth surface, consists of very dense indistinctly fibrillated connective tissue, which in diluted acids and alkalies swells up less strongly than ordinary fibrillar connective tissue. Key regards the nerve cushion as a colossal expansion of the neurilemma, and names it the nerve capsule.

The pale nerve fibres, into which the dark-bordered break up at their entrance into the nerve cushion, were first seen by Key. He admits, however, a more brush-like division of the nerve fibres into very fine varicose branches, and has not observed the frequently occur-

ring dichotomous divisions. Our description has been taken from fresh specimens placed in serum and diluted glycerine.

The *gustatory disks* are elliptical or circular sharply defined epithelial plates, with a transverse diameter of about 0·15 to 0·35 of a millimeter, and a thickness of 0·04 to 0·05 of a millimeter. Their inferior surface adheres firmly to the nerve cushion, whilst the upper forms the whole terminal surface of the papilla. The "nerve-epithelium," which composes the whole mass of the gustatory disk, is distinguished from the ordinary columnar and ciliated epithelium by the circumstance that it is optically perfectly homogeneous and very transparent, and is also very clear by transmitted light. When seen in thick layers, it presents a faint tinge of yellow.

It adheres more firmly to the papilla than the remaining epithelium. The cells also of which the disk is composed cleave to one another much more intimately and strongly than ordinary epithelium.

Leydig first called attention to the fact that the epithelium covering the free surface of the papillæ fungiformes differs from other epithelia. Later observers, with the exception of Fixsen, have uniformly corroborated this statement. Billroth, and especially Ernst Axel Key, have given full and minute descriptions of the nerve epithelium.

The gustatory disks of the Frog are composed of several kinds of cells, of which in all probability only one kind, the forked cells, are continuous with nerve fibres. Two other kinds, the broad goblet-cells and the slender columnar cells, appear to be more of an indifferent nature, like the investing cells of the gustatory cups. These three kinds of cells are so arranged in the gustatory disks, that the bodies of the goblet-cells form a single layer on the upper surface of the disk, whilst their central processes and the bodies of the columnar and forked cells form the inferior layer of the epithelium. Peripheric processes of the last-named cells, then penetrating between the bodies of the goblet-cells, run straight outwards to the surface of the gustatory disk (figs. 277 and 279).

The *goblet-cells* (Kelch-zellen), the number of which upon the larger papillæ amounts to several hundreds, are prismatic columnar structures, with five or six angles, caused by mutual

pressure. The body of these cells is from 0·02 to 0·024 of a millimeter in length, and 0·01 broad, with a vesicular nucleus in its lower third. Below the nucleus the cell bodies become attenuated, to form an irregularly shaped protoplasmic process. The cell body is enclosed by a firm membrane, having a wide opening above, like that of a goblet. This goblet is filled to the brim with quite homogeneous transparent protoplasm. Below, the membrane, gradually becoming thinner, and ulti-

Fig. 277.

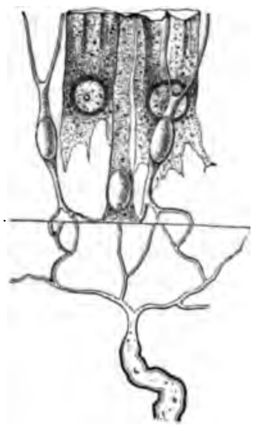

Fig. 277. Termination of the gustatory nerves of the Frog. Ramification of a nerve fibre in the nerve cushion, from a specimen prepared in glycerine. Group of two goblet-cells, one columnar and two forked cells, from a specimen prepared in chromic acid and glycerine. Magnified 600 diameters.

mately no longer demonstrable, is continued upon the process that likewise consists of perfectly homogeneous protoplasm. The processes of adjoining goblet-cells form by their juxtaposition, and perhaps also by their fusion, a plexus of protoplasmic substance in the deeper layer of the epithelium.

The goblet-cells were described by Key as modified epithelial cells. They are usually of uniform size. By the action of numerous reagents, as, for example, long maceration in iodine-serum, the protoplasm sometimes escapes from the cells, whilst the nucleus remains at the bottom,

and the thick cell wall in consequence forms well-marked longitudinal folds. By acids, especially acetic acid and perosmic acid, the protoplasm of the goblet-cells is rendered much more cloudy than the ordinary epithelial cells of the lingual surface. These cells must not be confounded with the so-called cup cells (Becher-zellen).

The *columnar cells*, of which several hundreds are usually seated on each papilla, consist of an ellipsoidal body, 0·006 of a millimeter long, and 0·004 of a millimeter broad, situated in the deepest layer of the epithelium, and immediately surmounting the nerve cushion. Towards the periphery, each is prolonged into an ordinary straight columnar process of about 0·032 of a millimeter in length, and 0·002 of a millimeter in thickness, which reaches to the external surface of the epithelium. The body consists of a thin investment of protoplasm around an ellipsoidal nucleus. The long cylindrical process is composed of very finely granular protoplasm, that appears to be surrounded by a thin membrane open above. The protoplasm of the cell body is extended usually in the form of a few short processes upon the surface of the nerve cushion. These processes never present the appearance of nerve fibres.

The columnar cells are no doubt in great part the "rod-cells" of Key. (See especially figs. 5, 7, 10, 11, *b*, *c*, *g*, of his work.) He associated them, however, with the forked cells—to be immediately described—of which only mutilated and imperfect examples appear to have fallen under his observation. I conclude that the long process of the columnar cells is enclosed by a membrane open above, from the circumstance that, as for example, in iodine and serum preparations it sometimes gradually flattens and becomes ribbon-like, whilst at the same time small masses of protoplasm protrude from the apex.

The *forked cells* (figs. 277 and 278), the number of which is, perhaps, double that of the goblet-cells, consist, like the gustatory cells of Mammals, of a body with long thin processes. The body has the form of an elongated ellipsoid, of 0·006—0·008 of a millimeter in its longest, and 0·003—0·004 of a millimeter in its shortest diameter, and is almost entirely filled by a vesicular nucleus with a central nucleolus. The processes spring from the peripheric and central poles of the bodies.

The peripheric process is in general furcate, and 0·021 to 0·030 of a millimeter long. Its ends reach the free surface of the epithelium. As in a fork, a handle and prongs may be distinguished. The handle is cylindrical, upon the average 0·0015—0·002 of a millimeter thick, and at most only 0·008 of a millimeter long, or it may even altogether fail. The shorter it is so much the longer are the fork prongs proceeding from it, and

Fig. 278.

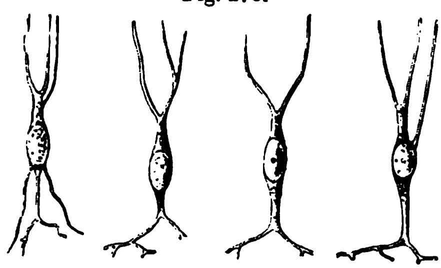

Fig. 278. Isolated fork-cells from the Frog (Rana temporaria). Magnified 600 diameters.

vice versâ. The handle divides into two, or more rarely into three, prongs, which sometimes again form secondary forks. Sometimes a third prong arises laterally from the handle. The apices of all the prongs lie in one plane, namely, the surface of the epithelium. The prongs are cylindrical rods of at most 0·001 of a millimeter in thickness, and closely resemble pale nerve fibres in their physical and chemical relations.

A single thick cylindrical process, having an average diameter of 0·0015 of a millimeter (or more rarely two or three more slender ones), arises from the centric pole of each fork-cell, and after running for at most a distance of 0·025 of a millimeter, and usually not more than 0·006 of a millimeter from the pole, divides into two branches. From these branches, smaller very delicate branches proceed, and again subdivide, which present the same appearance as the pale nerve fibres spreading over the surface of the nerve cushion, and are very probably continuous with them.

Mutilated fork-cells appear to have been seen both by Billroth

(fig. 12, *l*, *i*, *c*) and Key (figs. 7, *b*, 11, *a*, *d*, *e*). My description is chiefly taken from specimens that were teazed out with extremely fine glass needles, and were either quite fresh, and moistened only with iodine-serum, or which had been exposed for some time to a mixture of equal parts of strong glycerine and 0·4 per cent. solution of bichromate of potash. It was not uncommon for some of the processes to be broken off by this mechanical mode of isolating the cells. The transition of the centric processes of the fork cells into the nerve fibres

Fig. 279.

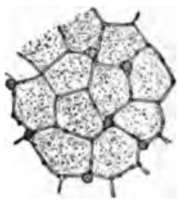

Fig. 279. Surface view of a portion of a gustatory disk from the Frog, after immersion for five minutes in a solution of iodine-serum. Several five or six-angled goblet-cells are seen from above, with the ends of a few columnar cells between them, and a great number of fork-cells in transverse section. Magnified 600 diameters.

which emerge from the nerve cushion, has not as yet been satisfactorily observed. This is chiefly owing to the circumstance that the methods which bring the nerves into view are not adapted for the demonstration and isolation of the fork-cells, and the two structures are therefore scarcely ever seen equally distinctly in the same preparation.

We may sometimes see very beautifully, as is shown in fig. 279, in fresh specimens, optical transverse sections of the prongs of the fork-cells in superficial views of the gustatory disks. They then appear as extremely small and bright circles, situated between the five and six-angled broad goblet-cells. We also see the apices of the cylinder-cells as somewhat larger dull circles, distributed amongst the goblet-cells.

c. Gustatory Organs of the Fish.

The gustatory apparatus of the Fish agree in all essential points with that of Mammals and of the Frog. Since the time of Leydig they have been known under the name of the

cup-shaped organs (*becherförmigen Organe*). They are bulbous structures, composed of peculiar cells, situated in the laminated epithelium of the skin and oral mucous membrane. At many points, cylindrical papillæ, containing nerves, project from the connective tissue lying subjacent to the cutis, or mucous membrane, into the epithelium, and a cup-shaped organ occupies the somewhat excavated summit of each.

Leydig, who discovered the structures in question in the external skin of fresh-water fishes, was inclined to regard them as tactile organs. F. E. Schulze has since clearly demonstrated them to be gustatory organs. He found that they were present in those portions of the palatine mucous membrane of the Fish, supplied by the glosso-pharyngeal nerve, and investigated their structure more minutely, discovering their close analogy with the gustatory apparatus of the Frog. The whole system of cup-shaped organs appears, according to Schulze, to be most developed in the cyprinoid fishes. The organs in question are here very closely placed in the palate, in the rudiment of the tongue, and on the mucous membrane covering the inner side of the bronchial arches, as also on the beard. They are somewhat farther apart on the lips, still farther on the skin of the head and of the rest of the body. They have not been observed on the lips of Cottus gobio nor in the external skin of the Pike, Salmon, Torsk, or Herring.

Each cup-shaped organ consists of a fasciculus of very long closely compressed cells that reach from the cutis or from the papillæ of the mucous membrane to the free surface of the epithelium. The length of these cells may be 0·1 of a millimeter or more. According to F. E. Schulze, two different types of cells may be distinguished in each cup. One of these corresponds to the investing cells of the gustatory bulbs of Mammals, and to the goblet and columnar cells of the gustatory disks of the Frog, and are chiefly situated in the peripheric part of the organ. They are long cylindrical cells obliquely truncated at their upper extremity, with their nucleus, which contains nucleoli, situated near their centre. Towards their inferior extremity, the cells, after becoming slightly attenuated, run out into a few slender finger-like or angular processes.

The second kind of cell, which corresponds to the gustatory cells of other Mammals, are most numerous in the central parts of the cup. These are very long slender cells, that consist of a small elongated elliptic body, with two thread-like processes. The body of each cell is almost entirely filled by a nucleus which contains distinct nucleoli in its interior. The peripheric process is far longer than the centric, but, like it, is an extremely delicate straight and cylindrical thread. The central process is frequently (after the action of a 0·5 to 1 per cent. solution of bichromate of potash) very regularly varicose. This is sometimes also seen in the peripheric process.

The connection of these cells with the nerve fibres that ascend in the papilla to the base of the gustatory cups, has not as yet been observed.

Future investigation must determine whether amongst the numerous sensory apparatus that are imbedded in the skin of many *invertebrate animals,* and which have commonly been regarded as tactile organs, some must be regarded as gustatory organs.

No details are known in regard to the *development* of the gustatory organs.*

Methods of Research.

For the investigation of the gustatory organs of Mammals, the lateral gustatory organs of the Rabbit and Hare may be recommended as appropriate for rapid demonstration. The knowledge of the coarser anatomical features, as the position, arrangement, number, size, etc., of the bulbs is acquired, as in the case of the gustatory papillæ, by dried preparations, and by the examination of sections which have been macerated in dilute acetic acid and glycerine. Or the specimen may be hardened for about twenty-four hours in perosmic acid, containing 0·5—1·5 per cent.; sections being then made which can be rendered transparent by glycerine. The freezing method can also be

* *Supplementary note.*—F. E. Schulze has very recently discovered cup-shaped organs in the papillæ of the oral cavity of the Tadpole, closely agreeing in their structure with those of the Fish. Perhaps these are the early stage of development of the gustatory disks.

adopted with good results. For the study of the minute anatomy of the bulbs, and of their component elements, the specimen should be macerated in iodine-serum (with or without admixture of a little chromic acid), then placed for a few days in solutions of bichromate of potash, containing 1—2 parts per cent., to which an equal volume of pure glycerine may be advantageously added. After such preparation, the specimen should be carefully broken up with very fine needles under the simple microscope. For this purpose I strongly recommend the use of extremely fine-pointed glass spiculæ, instead of the ordinary steel needles. The spiculæ can be obtained much more sharply pointed, and at the same time are much smoother and less adhesive than steel needles. In order to see the division and terminal distribution of the nerves, sections may be examined that have been made through dried or frozen preparations placed in diluted acetic acid and glycerine. Sections made through fresh, and especially through frozen, preparations, which have been further treated with chloride of gold containing 0·1—0·5 per cent., or with perosmic acid of 0·25—2·0 per cent., may also be recommended. For the fine terminal nervous expansion occurring in the mucous membrane close beneath the gustatory bulbs, Schwalbe recommends maceration for several days in chromic acid of 0·02 per cent., or in solutions of bichromate of potash containing 0·5 to 1 per cent.

The gustatory organs of the Frog should in the first instance be examined whilst still quite fresh, with the addition only of a little serum. By this means the peculiar epithelium of the gustatory disk can be recognized in the living state, the richly nucleated internal and the non-nucleated external layers are distinguishable, and the mosaic apparent on surface views from above, formed by the extremities of the large cup-cells and the points of the columnar and fork-cells, may be seen as well as the dark-edged nerve fibres and the other tissues of the papillæ. The breaking up of the gustatory disks into their elements is best accomplished by the aid of fine glass spiculæ under the simple microscope, in preparations which have macerated for a few days in a mixture of equal parts of solution of bichromate of potash containing 0·4 per cent. and strong glycerine, or which have lain for an hour in perosmic acidof 0·5 to 1·5 per cent. The branching of the nerves in the nerve cushion is sometimes beautifully distinct in fresh papillæ, if the gustatory disks have previously been separated in serum. They may then be rendered more distinct by the addition of glycerine ; perosmic acid should also be tried.

F. E. Schulze recommends, for the investigation of the cells in the

cup-shaped organs of the Fish, teazing out the tissues after a short maceration in a solution of bichromate of potash containing from 0·25 to 1 per cent.

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CHAPTER XXXIV.

THE ORGAN OF HEARING.

I. The External and Middle Ear, excluding the Eustachian Tube.

By J. KESSEL.

In the auditory organ of the more highly organised Vertebrata we may distinguish a sound-conducting and a sound-perceiving apparatus. The conducting apparatus includes the external and middle ear, whilst the sensory apparatus is contained in the vestibule, the semicircular canals, and the cochlea.

a. The External Ear.

This is represented by the auricle or concha, the external auditory meatus and the membrana tympani.

Auricle.—The auricle, with the exception of the lobulus, is essentially formed of elastic cartilage, the complex moulding of which confers upon it its peculiar shape. The cartilage itself belongs to the group of reticular cartilages; it is from one to two millimeters thick, and is invested by a perichondrium which contains a large number of elastic fibres. The fibres penetrate into the matrix of the cartilage, and form fine plexuses interweaving with one another, in the meshes of which small cartilage corpuscles are imbedded. (See Rollett, vol. i., p. 106, of this Manual.)

In regard to the muscles that are in connection with the concha, only those need here be mentioned that run between its several regions. These are small thin striated muscles that are inserted by means of short tendons into the perichondrium. The cutis of the concha, which is continuous with that of the

face and head, invests the cartilage, and at its inferior extremity forms a simple duplication known as the lobulus. Its whole surface is covered by lanuginous hairs, into the sacs of which sebaceous glands, having a diameter of from 0·5 to 2·0 millimeters, open. These last attain their greatest size in the interior of the concha, where, in comparison to the size of the hairs, they are very large and numerous, so that their openings are visible to the naked eye as minute fossæ. This relation is altered in many individuals at the entrance of the external meatus, where the woolly hairs are remarkably developed, on which account they have been named "tragal" hairs. Small sweat glands, of 0·15 of a millimeter, are chiefly found upon that surface of the auricle that is turned towards the skull.

The subcutaneous tissue of the external skin of the auricle does not everywhere present exactly the same features. It contains numerous elastic fibres which may be traced passing through the perichondrium as far as to the fibres of the reticular cartilage. On the concave surface of the auricle this tissue forms a thin lamina firmly attached to the perichondrium, on which account the skin is not here moveable. On the concave surface the subcutaneous tissue is more abundant, and the skin can consequently be moved hither and thither to some extent, and in the lobule and lower parts it contains fat cells in its meshes in gradually increasing proportion, by which means the form and thickness of the lobule, which it is well known possesses no supporting cartilage, is essentially determined.

The auricle derives its blood from various sources. The capillary plexuses proceeding from the arterial trunks ramify around the hair follicles and glands of the cutis and in the cartilage. A few of the vessels, according to Pareidt (31), traverse the cartilage obliquely from the inner to the outer side, whilst others remain in the perichondrium. Some of the latter, according to Meyer (28), give off minute branches that penetrate the cartilage, and ramify in its substance.

Nerves are found most abundantly on the convex surface of the concha. They are less numerous on the concave surface and in the lobule. The larger trunks accompany the larger vessels, and penetrate the mesial surface of the cartilage in order to reach the skin of the lateral surface.

EXTERNAL AUDITORY MEATUS.—The external auditory meatus presents a cartilaginous and a bony division, which together have an average length of twenty-four millimeters (Troeltsch, 45), of which eight millimeters belong to the first, and sixteen to the latter. The width of the meatus is subject to individual variations. The cartilaginous portion extends from the auricular cartilage and the tragus, and forms a channel or groove open behind and above, which is completed into a tube by fibrous tissue. It is moveably connected with the osseous portion of the meatus by a slender band of connective tissue. The cartilage itself presenting the same characters as that of the auricle, has, with a view to its greater moveability, upwards and backwards, towards the anterior and inferior wall, two fissures, the spaces of which are occupied by connective tissue. The cutis of the external auditory meatus is a continuation of that of the auricle and of the tragus. It is not everywhere alike, but exhibits differences in different parts, both in regard to its thickness and its internal structure. In the cartilaginous portion of the meatus the cutis is one millimeter and a half thick, is covered with woolly hairs, with which sebaceous and ceruminous glands are connected, and contains but little fat in the subcutaneous connective tissue; in the osseous portion the cutis rapidly alters, its thickness diminishing to 0·1 of a millimeter, the woolly hairs becoming finer and fewer in number, and the ceruminous glands, except upon the posterior and superior wall, are continued (though not in all instances) as far as the transition into the tympanic membrane. Beneath the epidermis are low papillæ arranged in longitudinal rows, and a corium containing much elastic tissue, the deeper layers of which represent the periosteum. The ceruminous glands agree both in the time and mode of their development, as well as in their external form and in their minute anatomy, with the sudoriparous glands. The same may be said of the contents of the ceruminous glands, so far as we may judge from a microscopical examination, except that the cerumen often contains confusedly aggregated pigment granules. (See this Manual, vol. ii., p. 597.) The ceruminous and sebaceous glands together furnish a whitish yellow, more or less fluid, secretion, that essentially consists of various-sized fat molecules, and a conglomerate of colouring particles and cells, in which last a

few fat molecules and pigment granules are imbedded; with these are mingled hairs and epidermis scales from the lining of the meatus, with particles of very various nature derived from without. When accumulated in considerable quantity, and allowed to remain for a long period in the meatus, the cerumen becomes altered in colour, and in consequence of the evaporation of its watery portion forms consistent masses, the so-called ceruminous plugs.

The larger arterial vessels run to the upper and posterior wall of the auditory meatus, and from these a large branch is given off, which is distributed to the membrana tympani.

The principal nerve trunks that were previously found in the cutis of the cartilaginous portion of the meatus break up in the osseus meatus into numerous branches, so that at the end of this passage the surface of expansion of the nerves, as compared with the outer parts, is considerably increased, which is in accordance with the great sensitiveness of these parts.

The *membrana tympani* is expanded like a septum between the external auditory meatus and the tympanum.

This membrane usually presents the form of an ellipse, the regularity of which is broken by the Rivinian hiatus or gap, which is situated anteriorly and to the upper part. The longer axis of this ellipsoid extends from behind and above, downwards and forwards, the shorter is directed from before and above, backwards and downwards. Corresponding to this, the diameter of the membrana tympani should be measured in the direction of the axes of the ellipsoid, and not, as is usually done, in the vertical and horizontal diameter. Different values are obtained in the two cases; in the former, when the longer axis of the ellipsoid is measured, it amounts to 9·5—10 millimeters, whilst the shorter is 8 millimeters; in the other case, the horizontal diameter is from 8—8·5, and the vertical 8·5—9 millimeters.

The planes of attachment of the tympanic membranes of opposite sides are inclined to one another; their inclination is indicated by angles opening above and posteriorly, the former divergence amounting to 130—135°, the latter having not as yet been satisfactorily determined. The membrana tympani itself does not lie in the plane of its attachment, but presents a curved surface, so that it forms a kind of funnel, the apex of which is situated at the lower part of the handle

of the malleus, and the meridianal lines of which are arched in a convex manner towards the cavity.

The examination of the intact membrane with low powers of the microscope will be found very serviceable in understanding the topography of its several constituent elements. With this object in view, the membrane should be prepared with the bony margins and the ossicula *in situ*, detached from the temporal bone, and placed for a few hours in water, when the cuticle which obstructs the view can be in great measure removed. The preparation is then to be deprived of water by immersion in absolute alcohol, rendered transparent by oil of turpentine, and allowed to dry. With the aid of low powers, three layers may now be distinguished, an external, a middle, and an internal, which are adherent by means of a thickened border, the tendinous ring, to a bony groove, which fails only at the Rivinian hiatus. The external layer, which is to be regarded as a continuation of the cutis of the auditory meatus, agrees essentially with this in its structure. The middle layer, which is the thickest of the three, consists of sharply defined fibres of various breadth, the greater number of which run either in a radial or circular direction to the malleus; only a small portion diverges between the two former in the most various directions. The radial layer lies externally beneath the cutis; the circular internally beneath the mucous membrane.

The *internal*, or *muco-membranous layer* of the *membrana tympani*, is an immediate prolongation of the mucous membrane of the tympanic cavity. It is very thin, and, on account of its complex structure, can only be distinguished with high powers. Although it is easy to demonstrate the different arrangement of the elements composing the tympanic membrane, an exception occurs at one spot, the Rivinian hiatus, respecting which there is still much difference of opinion. The bony groove into which the membrana tympani is inserted does not return into itself. A notch occurs in the bone, in the form of a more or less flattened abscission of the circle, the chord of which, having a length of 2·5 to 3 millimeters, is represented by the connecting line of the two ends of the

groove—the Rivinian hiatus. This notch is filled up by the tissue of the cutis and the mucous membrane of the tympanic membrane. The tendinous ring of the membrana tympani curves away, with the greater part of its fibres, from its direction at the two angles of the notch, and turns to the deeper-lying apex of the processus brevis into which it is inserted, whilst the remainder of the tendinous fibres of the ring extend upwards, and are lost in the connective tissue of the periosteum. In this way an irregular triangular space is formed, which is bounded above by the Rivinian notch, and on the two sides by two ligaments, by means of which the malleus, or rather the apex of its processus brevis, is attached to the anterior and posterior angles of the groove of attachment. The anterior ligament is 1·5 of a millimeter, the posterior 2 millimeters in length. The three points of insertion of these ligaments do not lie in a vertical plane, but the inferior point, which is connected with both the others, projects as far laterally beyond them as the short process of the malleus at this point pushes the membrana tympani towards the auditory meatus, so that a perpendicular struck from the Rivinian foramen downwards would cut off the malleus nearly at its neck. The distance from the highest point of the notch to the apex of the short process amounts to 2·5—3 millimeters.

The tissue which fills the just-described foramen, and which has been named the membrana flaccida by Odo Schrapnell (40), is less tensely stretched than the rest of the membrana tympani, and sometimes even projects like a pocket towards the tympanic cavity (Henle, 12). It consists of two thin layers, one of which is the continuation of the cutis, and the other of the mucous membrane of the membrana tympani. The cutis consists of an epidermis, beneath which are sinuous fasciculi of connective tissue, which extend obliquely over the triangular space from the posterior segment of the auditory meatus, to become continuous with the circular fibres of the anterior and superior segment, together with vessels and nerves. The layer of mucous membrane extends as far as to the osseous margin of the Rivinian perforation, and passes from this point to the neck of the malleus opposite to it.

The statement that the existence of a Rivinian foramen is quite

normal, is positively denied by Hyrtl (16) and others, who regard it as a consequence of inflammation. I have satisfied myself, in company with Dr. Gruber, of its occurrence both in the dead body, and also directly during life.

After this general account of the topographical relations of the membrana tympani, I proceed to the description of its finer microscopical characters.

The *cutis of the bony meatus* is continued upon the membrana tympani at all points of its circumference. The small hairs and glands sparingly present in the cutis are entirely absent over the membrana tympani; the papillæ extend only to the tendinous ring, except in the posterior superior part, where they reach as far as to the processus brevis. The rete Malpighii in the remaining segments of the membrana tympani exhibits a plane and only here and there wavy course. In a fresh membrana tympani, treated with perosmic acid, the corneal layer, just as in the meatus externus, becomes stained of a black colour precisely as far as to the epidermic layer of cells (a proof of the fatty nature of their ceruminous contents—Williams). The corneal cells and variously thick cuticle, as well as the corium, gradually diminish in thickness from the periphery towards the handle of the malleus, but attain their greatest thickness over its external edge. This is caused by the circumstance that the vessels and nerves of the cutis and of the membrana propria, accompanied by strong bands of connective tissue, extend towards the handle of the malleus in an oblique direction from the posterior and superior wall of the auditory meatus, and having reached it, cover it. Part of the bands of connective tissue encircles the handle of the malleus, and joins on the anterior side with that which invests the ascending veins of the malleal plexus.

Independently of the just-described general characters of the membrana tympani, the thickness of the epidermis is subject to manifold individual variations. It is a fact of general experience that the cells of the horny layer quickly become cloudy, and readily separate after death, so that in many instances we are not in a position to determine whether we have still all the layers before us, or whether

some of the more superficial have not become detached. It is obvious also that we must bear in mind the frequent occurrence of pathological alterations, in order to avoid forming an erroneous estimate of the normal thickness.

Independently, however, of these sources of error, I have satisfied myself by numerous measurements, that the thickness of the cuticle varies to a considerable extent in adults. How far the greater or less development of the cuticle of the membrana tympani affects the sensibility and the normal discharge of the physiological functions, cannot at present be stated with certainty. From analogy to the skin generally, we may however presume that the thinner the cuticle the greater the sensibility. The thickness of the cuticle of the membrana tympani in the new-born child favours the same view.

The *membrana propria* is composed of sharply defined, strongly refractive fusiform fibres, flattened laterally, and having a diameter of 0·0036—0·0108 of a millimeter. Under certain circumstances these appear to be homogeneous, though they are in reality fibrillated, as may be clearly demonstrated by the addition of various reagents, as chromic acid, chloride of gold, perosmic acid, etc. The fibres most closely resemble tendinous fibres, and present the same chemical characters, swelling up in solutions of potash and acetic acid, and becoming isolated by the solution of their cement in baryta and lime water. If the membrana tympani be boiled in dilute solution of potash, it dissolves, only a small quantity of elastic tissue remaining behind, of which part evidently belongs to the vessels, whilst part appears in the form of a continuous and very thin sheet, which probably forms the basement membrane of the mucous layer on the inner surface of the membrana tympani (Helmholtz, 11). The fœtal membrana tympani is particularly well adapted for the investigation of these fibrillated bands. We here find that the membrana propria is represented by distinct fasciculi of fibrils which present all stages of development. No distinct limits exist, in the earlier periods of development, between the connective tissue of the cutis and the fibres representing the subsequently developed membrana propria; the difference is first distinctly expressed towards the close of fœtal life.

The latter therefore (membrana propria) may be regarded

"as a deep layer of the corium favourably arranged and metamorphosed for physiological purposes." We may also see, in sections of the membrana tympani of adults, how the highly refractile fasciculi radiate out, and are continuous with the thin layer of fibrillar tissue of the cutis, and with the matrix of the mucous membrane. In consequence of the intimate connection of the fibrils by their cement, and their arrangement into strong broad bands, the latter offer a strong resistance to extension, and form, in the mode hereafter to be mentioned, an almost inextensible membrane, which as a mechanical arrangement for auditory purposes is, as Helmholtz (11) has shown, of the greatest importance. These fibres run in the several already mentioned layers, either parallel to one another, or decussating at very acute angles, and frequently communicate (Gerlach, 7), leaving everywhere lacunæ and larger spaces between them.

The lacunæ are usually empty, and are then bright and clear, or are covered at their borders with finely granular material. Sometimes nerve cells, in addition to the nerve fibres hereafter to be described, may be seen within them, exactly filling their cavities. These cells, called by v. Troeltsch (44) "tympanic membrane corpuscles," appear, according to the plane in which they are seen, sometimes in the form of fusiform, sometimes of stellate, bodies; in the former case being seen in profile, in the latter in face.

The larger lacunæ have nuclei attached to their walls, and are frequently filled with amœboid cells. By means of injections and the chloride of gold method, it may be demonstrated that such appearances are due to transversely and obliquely divided bloodvessels.

Near the periphery of the membrane the three layers of the membrana propria interweave with one another, leaving variously sized spaces for the passage of vessels between them, and by their further connection with the tissues of the cutis, of the external auditory meatus, and of the mucous membrane lining the tympanic cavity, form a thick swelling, "the tendinous ring," which is attached to the annulus tympanicus by means of a thin layer of periosteum. Between the highly refracting fasciculi of fibrils are found, besides the vessels,

fusiform nucleated elements, and not unfrequently small cartilage cells, either scattered or arranged in rows.

From the above description it appears that all the layers of the membrana propria are intimately connected with the tendinous ring. I must therefore corroborate Gruber (8) in his recently made statement, that the circular fibres can be distinctly followed into the tendinous ring; but may add, that they run at some distance from each other, and are severally given off at very acute angles from the latter. The fibres, as they are given off collectively in the vicinity of the ring, form groups, the thickness of which is equal to that of the epidermis, cutis, and mucous membrane collectively; by the tension of these fibres the radii of the surface of the tympanic membrane are rendered convex towards the auditory meatus. Towards the centre of the tympanic membrane the circular fibres diminish again in thickness, and are altogether absent at the lower third of the handle of the malleus and the adjoining parts. The circular fibrous layer is particularly well marked at the periphery of the anterior and superior segment, because the fibres here present, which proceed from the tendinous ring, become associated with those which come in an oblique direction from the posterior and superior wall of the auditory meatus, and extend across the already described triangular space below the Rivinian fissure.

Thus, with the exception of the above-mentioned neutral portion, the circular layer is everywhere present. The varying diameter of the circular layer, like the varying thickness of the cutis, which, as above stated, is most strongly expressed at the periphery and along the handle of the malleus, renders it impossible to give an average thickness to the membrana tympani. It amounts, in the two last-named spots, to about 0·1 of a millimeter; whilst in the intervening parts, where the cutis diminishes in thickness, and the circular fibres become thinner or are altogether absent, it is only half as much as this, or still less. Moreover, the membrana propria is attached to the handle of the malleus, but the views that are held upon the mode and nature of this attachment are widely divergent. According to v. Troeltsch (45), the handle of the malleus is introduced between the two fibrous layers (radial and circular

layers), the former proceeding from it, the latter lying behind it, yet in such a manner that the uppermost part of the annulus of circular fibres runs outwards from the malleus, and passes along its outer side. Grüber (8) subjected the mode of attachment of the malleus to the membrana tympani to fresh examination, and described a till then unknown cartilaginous structure which commences above the short process, and extends for half a millimeter below the handle. The cartilage is firmly attached to the lower two-thirds of the manubrium; but above, where the processus brevis is present, it is not attached, but forms a kind of joint, the cavity of which is filled with a synovian-like fluid. Still more recent examinations of this part made by Prussak (36), myself (17), and Moos (29), agree in showing that a third part of the processus brevis consists of cartilage, which, however, passes uninterruptedly into the osseous portion. According to Prussak and Moos, a thin layer of cartilage cells is also to be found beneath the entire periphery of the periosteum of the manubrium, not only in the new-born child, but in adults and old persons.

I have very recently repeatedly studied this part in tympanic membranes that were still in connection with the malleus, and taken from persons of different ages. In embryoes, from the third to the ninth month, the ossicula are still in the condition of cartilage, and have the advantage of being fit for section without preparation, whilst those of newly born children and of adults require to be first subjected to some decalcifying process. If sections be so made as to exhibit the membrana tympani and the malleus in their natural connection, the malleus appears (with especial distinctness in embryoes) to be invested by a periosteum quite independently of the membrana propria, and to be only in connection with the latter by a duplicature of the mucous membrane, having a breadth of 0·2 to 0·3 of a millimeter. At the point where the processus brevis is subsequently developed, a cluster of highly refractile nucleated cells occurs, lying above the periosteum, and in the substance of the duplicature. These elements, persisting throughout life as cartilage cells, form a mass intimately connected with the bony part of the processus brevis, which develops towards the end of fœtal life with coincident

ossification of the periosteum at the point of fusion. About this time also the connection of the malleus with the membrana tympani is very intimate, though only at two points; namely, at the processus brevis, where the ligaments extending from the borders of the Rivinian gap are inserted into it, and at the lower third of the manubrium, where a portion of the radial fibres give additional strength to the periosteum, whilst the others decussate in front of the manubrium, in order to become continuous with the irregular layer found between the radial and circular fibres. The membrana propria is only connected with the periosteum of the upper part of the manubrium by means of loose connective tissue, so that a slight capability of movement exists at this part also, without any kind of articulation being present. The mucous membrane as it passes from the inner surface of the membrana tympani to the malleus is scarcely perceptible at its attachment to the former.

The statement that the tympanic cavities are filled throughout the *whole* of intra-uterine life with young connective tissue requires corroboration, as I have frequently found them filled with fluid in old embryoes and new-born children, their mucous membrane being at the same time coated with epithelium.

The mucous membrane of the membrana tympani is composed of an epithelium resting on a fibrous matrix. The epithelium which has hitherto been described as consisting of a simple layer of pavement epithelium, by no means presents this character throughout, but has the same peculiarities of form as that described by Ludwig and Schweigger-Seidel (48) in the epithelium of the abdominal surface of the diaphragm in the Rabbit. After treatment with nitrate of silver, polygonal areas of various size, enclosed by dark sinuous lines, come into view on the surface of the mucous membrane, as is seen in fig. 280. Where these lines meet, more or less round or angular spots appear (*d*) which give the impression of openings, an impression that is strengthened by the circumstance that they appear to be homogeneous after treatment with iodine-serum. The polygons may be distinguished as large (*a*), small (*b*), and smallest (*c*); the latter lying in particular along the manubrium and towards the periphery, and enclosing the most homogeneous

spaces. The colouring of the cells under the influence of solution of nitrate of silver varies, some scarcely appearing to be at all stained, whilst others are black and opaque, the latter chiefly occurring in the smaller polygons. The nuclei are here, as is common after treatment with nitrate of silver, invisible, though a few scattered ones are sometimes perceptible, usually occupying an excentric position.

Fig. 280.

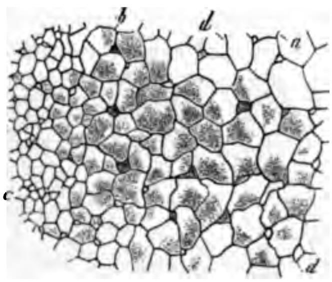

Fig. 280. Epithelium of the mucous membrane of the membrana tympani of Man. Silvered preparation.

The fibrous framework or matrix of the mucous membrane is subjacent to the just-described epithelium, and on the other hand rests upon the membrana propria. The arrangement or disposition of the fasciculi in the membrana tympani of Man is subject to variation. Fig. 281 consequently only gives a representation of the form of the framework as it is most frequently met with in the posterior segment of the membrana tympani. Between the manubrium and the tendinous ring the membrane is composed of very fine fibres, forming more or less broad trabeculæ of similar structure that run in various directions. The membrane varies in thickness. It usually extends on the one side as far as to the manubrium, with the mucous membrane of which it is continuous, or it already terminates at some distance from it, and is then continued by means of several trabecular processes over the radial fibres, which two last interweave together. I have usually observed a few trabeculæ of the framework extend to the processus brevis. On the other side, towards the tendinous ring, trabeculæ pass from the cen-

tral membranous expansion to the periphery, and streaming out over the circular fibres like a fan interweave with one another. Owing to the radiation of the adjoining trabeculæ, the margin of the middle membranous expansion forms a series of curves, the concavities of which are directed towards the periphery. Owing to their peripheric attachment, these arches leave hiatuses varying in their number, form, and position. The central membranous expansion may also exhibit similar gaps. The structure of the framework is further rendered

Fig. 281.

Fig. 281. Part of the posterior segment of the membrana tympani, seen with a low power. *a*, The membrane itself lying beneath the epithelium, with its processes stretching towards *b*, the tendinous ring; the dark plexus represents bloodvessels. From a specimen stained with chloride of gold.

complicated by the circumstance that the above-mentioned radiating trabeculæ do not all lie in the same plane; some, instead of going towards the tendinous ring, penetrate deeply between the radial and circular fibres into the above-described free spaces remaining between the circular fibres, and expanding here form a trabecular tissue, so as to leave a number of spaces

or "lacunæ" which intercommunicate with one another. These again, by means of spaces existing between the circular fibres, may stand in connection with the upper system of cavities. These spaces are all lined with an endothelium, the form and instability of which renders it most comparable with the epithelium lining the layer of Descemet on the posterior surface of the cornea. After treatment with solutions of silver and of gold, dark-coloured looped lines forming meshes are brought into view, similar to those characterising the interior of the lymphatics. The relations of the framework to the remaining parts of the membrana tympani, it is to be observed, are such that the anterior part normally presents a similar configuration to that just described, whilst it only appears as a foraminated membrane in the lower parts. Yet, even here, the already-described variations in the arrangement of the fibres may also occur.

Gruber, in a monograph (8), attributes a dendritic structure to a fibrous framework, the position of which indeed corresponds with ours, but the minuter details of which he has not sufficiently described.

In connection with the fibrous framework, and especially in children, at the marginal zone of the mucous membrane, villous processes, 0·220 of a millimeter in length, and 0·088 of a millimeter broad, were first described by Gerlach. (These villi occur also in the purse of Troeltsch and at the malleus.) They are invested with pavement epithelium, and are composed internally of connective tissue in which are seen capillary loops.

In regard to the nerves, the bloodvessels, and the lymphatics of the membrana tympani, the relations of the bloodvessels alone are known through the labours of Gerlach (7), v. Troeltsch (45), and Rüdinger (38). In reference to the nerves, v. Troeltsch states that they are chiefly or almost entirely distributed in the cutis, without, however, giving any further account of their mode of termination; he was never able to discover them in the mucous membrane; but Gerlach (7) once or twice recognized in the latter region a few fine, non-medullated nerve fibres.

The membrana propria, in accordance with the observations of all who have hitherto studied its anatomy, is destitute of

nerves and vessels; a few capillary vessels only, according to Gerlach (7), forming anastomoses at the periphery between the mucous membrane and the cutis. As far as I am aware, no other description of the lymphatics exists besides that published by me in the *Centralblatt für die Medicinische Wissenschaften*. The results of my observations show that nerves, bloodvessels, and lymphatics are discoverable in all the three principal layers forming the membrana tympani—the cutis, the membrana propria, and the mucous membrane.

The *bloodvessels* of the cutis (and membrana propria) are chiefly supplied by an artery which runs from the posterior superior wall of the auditory meatus on to the membrana tympani, ascends at its posterior part along the manubrium, and gives off a successive series of small branches in a radial direction. The artery crosses the lower extremity of the manubrium, and then divides into two branches, of which one supplies the anterior inferior quadrant. The branches running in a centrifugal direction in the cutis, and here and there connected by transverse or oblique anastomoses, terminate in capillaries, which on the one hand unite to form the smaller veins accompanying the arteries, and on the other hand pass straight into two venous plexuses, of which one encircles the manubrium, and conveys its blood into the posterior superior veins of the cutis of the auditory meatus, whilst the other lies at the border of the membrana tympani, and likewise conveys its blood in an outward direction.

In addition to this main artery, other smaller ones pass, at tolerably regular distances from the periphery, with the cutis, upon the membrana tympani, where they quickly break up into capillaries that join with those above described. The capillary plexus lying centrally in the membrana propria communicates both with that of the mucous membrane, and with the more external one just mentioned; it is distributed between the radial and circular fibrous layers, as well as in the lacunar system, being everywhere closely attached to the walls of the latter. At the middle and internal parts lying between the manubrium and the tendinous ring, where the radial fibres become more and more aggregated together in their course towards the manubrium, and the circular fibres are deficient,

the capillaries pass more transversely or obliquely from the exterior between the radial fibres to the internal plexus of the mucous membrane, so that this spot appears to be the least vascular part of the membrana tympanum. Towards the periphery the radial fibres diverge from one another, leaving grooves or channels between them that are filled by capillaries which quickly increase in size; the vessels themselves, therefore, also run in a radial direction and at regular distances from each other. These vessels also pour their contents into the marginal plexus.

If the cutis and the mucous membrane be detached from the membrana propria, the transversely and obliquely traversing vessels are torn through, and then the above-mentioned spaces with adherent nuclei come into view.

The inner blood vascular plexus of the mucous membrane consists essentially of capillaries, and is chiefly distributed as a close plexus of vessels around the manubrium and about the tendinous ring. The plexus of the last-named part is to be regarded as a prolongation of the capillaries of the mucous membrane of the tympanic cavity. These run on to the membrana tympani, there form loops around or entirely encircle the foramina between the trabeculæ, and then turn back to the vessels of the tympanic mucous membrane, or extend to the borders of the tunnel-like passages, or penetrate directly into the deeper layers in order to anastomose with the capillaries of the membrana propria. The plexus surrounding the manubrium, and also connected with the median and the above-described plexus, obtains its blood from a few small arteries which run from above downwards in nearly the same direction as the arteries of the cutis.

As we have just seen, the blood of the tympanic mucous membrane is carried off in two ways—by the veins of the tympanic cavity, and by those of the external auditory meatus. The chief proportion of the blood traversing the arteries of the membrana tympani and the capillaries may therefore enter the larger veins by very different routes; by a shorter path into the plexus of the malleus, and by a longer path over the membrana tympani into the marginal plexus. The path traversed by the blood during life will obviously depend upon the nature of the resistance with which it meets in the different veins. It

may however be said with certainty that the arterial blood always returns by the shortest route through the plexus around the manubrium, when no special obstacle is presented to its course, in the veins into which the vessels of this plexus discharge themselves (Prussak, 37). I have satisfied myself of the accuracy of this last statement, which was advanced by Prussak from the results of his carefully performed injection experiments. As I cannot here enter into any details respecting the means and methods which have led me to this conclusion, I shall content myself with a statement of the method I have employed to demonstrate the circulation of the membrana tympani. I subjected frogs to the influence of woorara, and having divided the masseters, drew back the lower jaw as far as possible. The animal was then so placed between moist cushions upon a glass plate, that the external surface of the membrana tympani to be examined lay upon the plate, and was then pinned down to the stage of the microscope. Owing to the short and wide Eustachian tube of the Frog, the circulation of the various portions of the membrana tympani may then, by judicious turning of the head, be very well studied.

In regard to the *lymphatics* it may be broadly stated that, like the bloodvessels, they are arranged in three layers. The first belongs to the cuticular investment; the second to the membrana propria; and the third to the mucous membrane. In the cutis they form an extremely fine plexus lying immediately beneath the rete Malpighii, the vessels of which accompany and frequently arch over the blood capillaries. They gradually pass into wider capillaries, which often cross the blood capillaries, and ultimately collect into separate larger trunks, which either run backwards and upwards, or extend like the bloodvessels at various parts towards the periphery and the auditory meatus. In the mucous membrane a sparingly distributed subepithelial plexus is found chiefly in the vicinity of the tendinous ring, which is distinguishable from the bloodvessels of equal width by its manifold dilatations. The vessels penetrate into the lacunar system through the above-described spaces in the fibrous framework, and there form large spherical and saccular dilatations. (See fig. 282.)

These last again are continuous with capillaries of small diameter presenting valve-like constrictions, which either communicate with the above-mentioned deeper-lying funnel-shaped

trunks, or pass straight through the membrana propria, so that by this means all the three layers of lymphatics belonging to the membrana tympani intercommunicate with each other and with those distributed in the cutis of the external auditory meatus. It is further to be remarked, that after brushing off the epithelium of the mucous membrane, and treatment with nitrate

Fig. 282.

Fig. 282. Lymphatics with their saccular dilatations lying immediately subjacent to the fibrous framework of the mucous membrane. From a specimen prepared with solution of nitrate of silver.

of silver, a system of serous canals comes into view, both upon the immediately subjacent membranes and trabeculæ, and upon the depressions and tunnel-like passages lying between them, as was first described by Recklinghausen in the diaphragm of the Rabbit. (See vol. i., p. 304.) This is distributed over the whole surface of the membrana tympani, but especially over those parts where the membrane is covered with small-celled

epithelium, and therefore along the manubrium and towards the tendinous ring. Here they frequently increase in size and number at the expense of the brown-coloured masses, and form light spaces communicating with each other.

I found in the clear spaces of the membrana tympani of the Dog and Cat, as in that of Man, strongly looped fine lines, thickened at certain points, which, becoming progressively finer by dichotomous division, run outwards in all directions. and consequently into the brown masses. (See fig. 283.) Similar markings, indicating the presence of serous canals, have been described by Koster,* and used by him as corroborating his view, that the serous canals are formed of epithelial cells. The light spaces are here and there seen bounding one or both sides of the vessels, and communicating with the attenuated extremities of adjoining serous canals. What relation exists between the serous canal system and the epithelium of the mucous membrane, or rather between it and the above-described openings between the epithelial cells, I have not hitherto been able to discover; and shall here only mention the interesting fact in a physiological point of view, that in the Dog I effected the most beautiful and complete injection of the lymphatics of the membrana tympani from the tympanic cavity, by the method first adopted by von Recklinghausen, and subsequently by Ludwig and Schweigger-Seidel, in the case of the diaphragm. It follows, therefore, from the above injection experiment showing the arrangement of the lymphatic system, that every alteration of tension of the membrana tympani must exert a suction action on the contents of the tympanic cavity, and eventually also aid the propulsion of the same within the lymphatics.

The *nerves* of the membrana tympani are distributed like the vessels in the cutis, membrana propria, and mucous membrane. The larger trunks accompany the principal blood-vessels, divide like these, and frequently intercommunicate like the capillaries. They extend with the latter into the regions supplied by them, and consequently form close plexuses both

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* *Ueber die feinere structur der menschliche Nabelschnur.* "On the Minute Anatomy of the Umbilical Cord of Man." Inaugural Dissertation. Würzburg, 1868.

beneath the cuticle of the dermis and the epithelium of the mucous membrane. We may thus distinguish here a basal, a capillary, and a subepithelial plexus.

A principal nerve trunk, which consists of medullated fibres provided with the sheath of Schwann, and lies between the cutis and the membrana propria, passes from the auditory meatus to the membrane at the upper part of the posterior segment close to and behind the artery, giving off branches

Fig. 283.

Fig. 283. Serous canals of the membrana tympani of the Dog.

which accompany the vascular twigs. In correspondence with the forking of the artery over the manubrium of the malleus, the nerve divides into two branches, of which one supplies the anterior, and the other the posterior and lower part of the membrana tympani. Besides this main trunk, several smaller nerves accompany vessels passing to the membrane from various parts of the periphery. The coarse branches of all these nerves which lie between the cutis and membrana propria, I have named the "fundamental plexus of the membrana tympani."

The branches given off from the trunks break up into numerous fibres, which, though non-medullated, are yet provided with sheaths, and these form wide plexuses around the

vessels, as well as in the interstices between the capillaries. If we inspect such a plexus more minutely, we see that the several fibres are closely adherent to the capillaries, but occasionally run at some distance from them, so that a small clear space becomes apparent between the margins of the nerve and vessel. In its further course the nerve may leave the vessel altogether and join with the plexus found beneath the rete Malpighii, or it may break up at once into very fine fibres which encircle the capillaries.

Lipmann* and Tomsa† have given a similar account, but, like myself, have been unable to trace any connection between the nerve fibrils and the nuclei of the capillary wall.

Fig. 284.

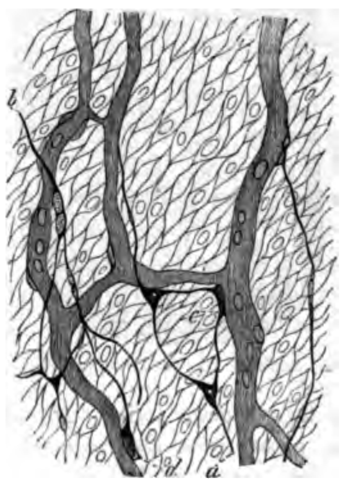

Fig. 284. Nucleated nerve fibre which is attached to the capillary wall at *d*, by a pyriform enlargement. From a specimen taken from Man, and prepared with chloride of gold.

A second kind of nerve fibres do not present the above detailed characters, but appear as simple axis-cylinders which are enlarged at many points of their course into nodal swell-

* *Inaug. Dissert.* Berlin, 1869.

† *Centralblatt für die medecin. Wissenschaften,* No. 39.

ings containing a distinct nucleus. From such an enlargement two or more fibres may be given off, in the latter case giving it the appearance of a small ganglion cell. I have seen such fibres enter into close relation with the cells of the rete Malpighii, and also with the vessels lying close beneath the rete. In successful preparations we may see these nerves lying as above described, with their nucleated enlargements closely applied to the capillaries, and again becoming detached and running at some distance from them (fig. 284).

Elsewhere they may be traced into fine fibres which in their further course sometimes exhibit pyriform enlargements. These last, after treatment with chloride of gold, assume a darker tint, whilst the neighbouring nuclei of the capillaries usually remain clear. In gold preparations it appears as if the pyriform enlargement were situated in the angle of a forked division of the nerve, so that one arm terminates by a capitate extremity in the dilatation, whilst the other forms a delicate thread on the side turned towards the capillary wall, and terminates on the vascular wall in a manner that is still unknown (fig. 284, *d*).

Hitherto, therefore, no satisfactory evidence has been adduced to show that these dilatations constitute the ends of the vascular nerves, since they themselves give off fibrils which are lost on the vascular walls. The relations just given can indeed only be perfectly demonstrated in a few instances; for the long course the nerve fibres pursue to the point where they expand into a brush of extremely fine fibres, permits satisfactory evidence of their continuity with the pyriform enlargement to be furnished only in very fortunate preparations.

It has been remarked above, that only a part of the nerve fibres are distributed upon the bloodvessels, another part becoming connected with the plexus lying in the rete Malpighii. This last forms a plexus provided with bi- and multipolar cells, situated immediately beneath the deepest layer of the epidermis. From these plexuses extremely fine but distinctly recognisable fibrils are given off, which often run directly between the cells, so that a doubt may arise whether we are looking at a cell border or a fibre of this kind, but which may also be frequently traced without any confusion

over the cell margins, as well as over the nuclei, to reach adjoining or more distant cell-layers. I am unable to make any positive statement as to their mode of termination.

Before passing to the consideration of the middle layers of the membrana propria, it may here be mentioned that numerous nerve fibres proceeding from the basal plexus penetrate between the fibres of the membrana tympani, and either pursuing a tortuous course, or undergoing continual dichotomous division, apply themselves to the tendinous fibres, or traversing the spaces and lacunæ between these, are distributed as nerves of the mucous membrane. In these territories of distribution nucleated nodal enlargements similar to those above described also occur.

Thus we have found in the membrana propria certain fissures and vascular openings, with their just-mentioned contents, and in addition a large number of nucleated enlargements provided with two or more processes which are connected with the nerves there distributed, and are placed over and between the several layers of fibres. I once more adduce these facts, because up to the present time all cellular elements found between the fibres of the membrana propria have been considered to be connective tissue, whilst in truth, as the above description shows, only a small number of them belong to that tissue, and the greater part must be regarded as belonging to the blood and lymphatic, or to the nervous system.

Lastly, in regard to the nerves of the mucous membrane of the membrana tympani, I must first observe that they are by no means so sparingly distributed to it as has been hitherto maintained. Here also we find a vascular plexus and a subepithelial plexus. The former accompanying the lymphatics earlier than the bloodvessels, obtains its fibres partly from the plexus tympanicus, by means of twigs which pass to the membrana tympani at various points of the periphery together with the mucous membrane of the tympanic cavity, and partly from those nerves which lie in the cutis, by means of fibres that perforate the membrana propria. It distributes its branches on the one hand to the capillary bloodvessels and lymphatics, and on the other hand to the subepithelial plexus.

The latter forms a fine plexus immediately beneath the epithelium, supplying this last also with fibrils.

b. The Middle Ear.

The term middle ear includes (1) the tympanic cavity, with the ossicula contained in it, and their muscles and ligaments; (2) the cells of the mastoid process; and (3) the Eustachian tube.

The Tympanic Cavity.—The bony walls of this cavity, the structures found in it, as well as the inner surface of the membrana tympani, are covered by mucous membrane, which is continuous with that lining the Eustachian tube, and at the same time passes through the antrum mastoideum into the cells of the mastoid process. The mucous membrane of the tympanic cavity of Man is, speaking generally, composed of an epithelium and a subjacent layer of connective tissue.

The epithelium presents various forms. On the floor and lower portion of the anterior, internal, and posterior walls of the cavity it consists chiefly of ciliated columnar cells; on the promontory, the roof, the membrana tympani, and the ossicula, it is tesselated (v. Troeltsch, 45). The transition of the former into the latter is gradual, the ciliated columnar cells becoming lower, and passing into tesselated ciliated epithelium, and finally into non-ciliated pavement cells. If the columnar epithelium be separated from the subjacent tissue, and an attempt be made to isolate the cells, cup-cells are found resembling those of the intestinal mucous membrane, together with columnar cells both with and without nuclei, of which the non-nucleated possess an extremely slender and often rod-shaped body, and a slender brush of cilia which are often adherent to each other. Both forms are continuous below with homogeneous strongly refractile fibres. They are sometimes forked at their lower extremity, and are then in connection with two such fibres. In a specimen prepared by teazing, I have succeeded in isolating a cell with two processes, of which one still remained in connection with a fibre three times the length of the cell, which could be traced beyond this for some distance into the connective tissue.

B 2

On moving the covering glass, the cell with the fibre floated freely in the mounting fluid, so that it was impossible to entertain any doubt of their connection. Rüdinger also described fibres in the mucous membrane of the tuba Eustachii, continuous on the one hand with the epithelial cells, and on the other hand with the tissue of the submucosa.

Besides these forms of columnar cells, there is another fusiform variety characterised by the nucleated body of the cell becoming attenuated as it extends both upwards and downwards. The upper process extends to the epithelial margin; whilst the lower is columnar, with a bright highly refractile fibre, which is lost in the subjacent tissue, and not unfrequently presents a nodal enlargement near the cell from which it proceeds.

In regard to the pavement epithelium, it may here be observed that wherever it occurs it presents the same peculiarities of form as that which has been already described as covering the mucous membrane of the membrana tympani. If the epithelium be detached, and the mucous membrane be treated by the silver method, serous canals come into view; but if the epithelium be not removed, and a solution of chloride of gold or perosmic acid be poured over it, dark red or black stellate intercommunicating lines appear (with especial distinctness in the Dog and Cat) immediately beneath the epithelium, which are here and there continuous with broad and similarly dark-coloured striæ that are lost in the deeper layers of the tissue. The question whether these last are to be regarded as identical with those brought into view by nitrate of silver, and whether like them they may be in intimate relation with the lymphatics, must at present remain open, as I am unable to adduce any positive evidence in favour of either view.

Two layers can be distinguished in the subjacent stratum of connective tissue, an upper lying immediately beneath the epithelium, and a lower, which represents the periosteum, and at the same time gives off fibres to the sheaths of the nerves running in the grooves of the bone, as well as in the tunica adventitia of the vessels of the bone. The upper layer forms a fibrous framework, which is to be regarded as the prolongation of that I have more minutely described in the membrana

tympani, and which here presents the same relations to the periosteum as it there does to the membrana propria. Here also it consists of extremely minute fibrils, which collectively form a framework of trabeculæ and a foraminated membrane, which, like the periosteum, includes large spaces filled with nerves, bloodvessels, and lymphatics. At various points of the cavity this fibrous framework becomes detached from the periosteum, in order to stretch across the cavity from one bony prominence to another. These bridges serve at the same time as supports for numerous capillaries running from point to point, and are everywhere covered by an epithelium which is continuous, where they are attached, with that of the mucous membrane. Thereto belong the ligamentum mallei superius, the ligamentum mallei externum et posterius, and the posterior pocket of the membrana tympani. The ligamentum mallei anterius is composed of thick bundles of fibrils resembling those of tendinous tissue, and forms with the ligamentum mallei posterius the so-called axial cord, which at the same time constitutes the axis of revolution of the malleus (Helmholtz, 11). Moreover certain trabeculæ which are stretched between the numerous bony processes on the floor of the tympanic cavity belong to the same category. A trabecular framework which I have very frequently found in the vicinity of the stapes is deserving of special mention. This passes from the eminentia pyramidalis, which is a bony projection, to the semi-canal of the tensor tympani—projecting sometimes strongly into the free space of the tympanic cavity —and forms a more or less deep groove or nick with the posterior superior margin of that canal. Proceeding from the free border of this band I frequently saw several trabeculæ, often communicating with each other, span the groove, and pass to be inserted either at the base or into the posterior crus of the stapes.

Peculiar bodies, differing considerably from each other in external form and size, but upon the whole exhibiting the same structure, present themselves in this framework, as well as on the floor of the tympanum and in the ligamentum mallei superius, which extends from the tegmen tympani to the caput of the malleus. In the more simple forms of these

bodies we may recognize on the one hand a central axial band, and on the other a series of capsules arranged concentrically round it. The axial band appears in the form of a smooth round cord, which, after running free for a variable distance, enters at one pole of the lemon-shaped body, and emerges again at the opposite, to expand immediately in a fan-like manner in the above-described foraminated membrane of the mucous membrane. Without the addition of coloured substances, this shows an extremely fine fibrillar structure, with a cloudy finely granular material between the fibrils; but if it be treated with solutions of silver or gold, it becomes more deeply tinted than the tissues of the capsules. The capsules arranged concentrically around the axial band have likewise a fibrillar structure. Between the several capsular layers are spaces which either appear homogeneous or are filled with fusiform elements. The margins of the spaces are frequently covered with a finely granular cloudy material. The outermost of the capsules often presents a regularly wavy course, and possesses a delicate pavement epithelium on its external surface. At one pole of the body this capsule forms a circular highly refractile ring, which leads into a funnel-shaped depression occupied by the axial band at its point of entry; at the other pole the capsule is continued upon the axial band as it emerges. The description just given corresponds to the simpler types of the bodies, which, apart from the structure of the axial band, present the appearance of a Vater's corpuscle. But other forms are also met with; a structure of similar character may be so constructed as to present a figure of 8, whilst it may either be straight or bent at an angle. In both cases it gives the impression of two of the above-described bodies being so connected together that the two capsules are continuous with one another at the point of union. In other instances, again, we may see the axial band divide into several branches after its emergence, which may again bear other smaller corpuscles of the same kind. Fig. 285 is an illustration of a body of this kind, which I found stretched between the base of the stapes and the band proceeding from the eminentia pyramidalis. These organs, as we shall hereafter see, occur also in the mucous membrane lining the mastoid cells, but never attain so remarkable a size

in that position as in the tympanic cavity. The corpuscles may be either roundish, or elongated, or fusiform, and are found of all sizes, from microscopic minuteness, 0·08 to as much as 0·5 of a millimeter in length.

Though I am not in a position to determine the histological significance of these corpuscles, in a physiological point of view their presence in the trabeculæ, and the intimate con-

Fig. 285.

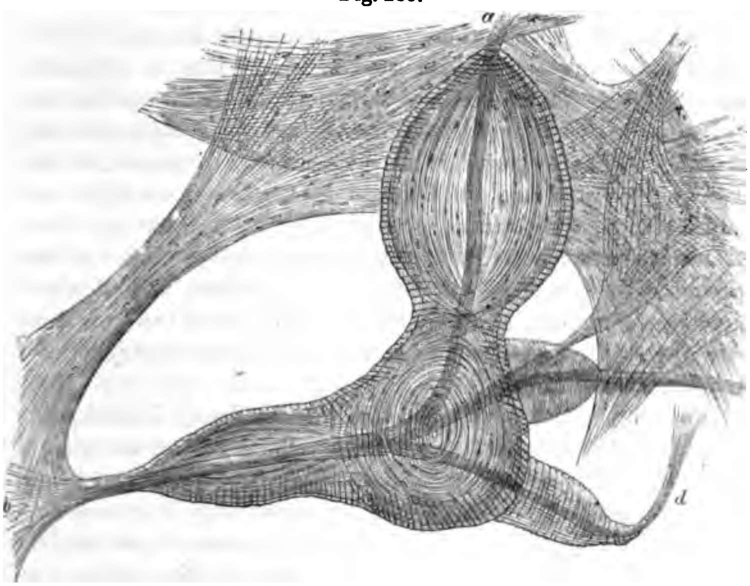

Fig. 285. *a*, Point of entrance of the axial cord; *b*, point of passage into a membrane; at *c* and *d*, branches of the angularly bent axial cord are shown with smaller corpuscles.

nection of the latter with each other, as well as with the mechanical apparatus for the conduction of sound of the middle ear, seems to indicate that they participate to a certain extent in the auditory processes; but the precise determination of this must be referred to the experimental physiologists.

These corpuscles were first discovered by v. Troeltsch * in the

* Virchow's *Archiv*, Band xvii., p. 60, 1859.

mucous membrane of the tympanic membrane of an old and deaf woman, and were regarded by him as pathological formations. Their importance as physiological structures was first recognized from my own researches and those of Politzer (34 and 35).

The mucous membrane of the tympanic cavity receives its supply of nourishment from various quarters and from different *arteries*. The principal artery pursues a very tortuous course on the floor and over the promontory. The branches it gives off often form circular and elliptical loops, and then break up into a plexus of *capillaries* lying beneath the epithelium, which transmits the blood traversing it into a subjacent capillary plexus, the vessels of which rapidly increase in size, and again discharge their contents into the comparatively large veins of the periosteum. The arterial branches do not always present these relations, since many run straight and undivided till they suddenly break up into capillaries, which often pass in considerable numbers between the fibres of the foraminated membrane, in the same direction, and at equal distances from one another, transmitting their contents into large *veins* lying on the floor of the above-described system of cavities.

The *lymphatics* of the mucous membrane lining the tympanic cavity exhibit the same relations as those of the membrana tympani. They form in Man, in some parts, a system of tubes, either presenting spherical dilatations, or large lateral diverticula, which is chiefly situated in the periosteum, or which, after presenting saccular expansions, opens out into the lacunar system. This tubular system is not however everywhere present, but is in some parts, as upon the upper bony walls and roof of the cavity, replaced by funnel-shaped or spherical and intercommunicating spaces, which are again traversed by a fine plexus; appearances that are also presented in the tympanic cavity of the Dog, as shall presently be more fully described. I have frequently found these spaces clogged with white blood corpuscles, which makes them resemble the follicles of a gland. These appearances have probably led to the statement made by Nasiloff, to the effect that he had discovered a lymphatic gland in the mucous membrane of the tympanum, at the part where it passes from the upper wall of the cavity to the

membrana tympani. As to any other relations of the lymphatics to the epithelium of the mucous membrane, I have no further information than that above given, respecting the figures which make their appearance beneath the epithelium after treatment with solutions of silver and gold.

The *nerves* which are distributed in the mucous membrane of the tympanic cavity, and of the membrana tympani, and which may also be followed into that of the Eustachian tube, and into the cells of the mastoid process, proceed from the plexus tympanicus, which is an anastomosis between the otic ganglion, the petrosal ganglion of the glossopharyngeal nerve, and the carotid plexus; that is to say, the superior cervical ganglion of the sympathetic nerve (Bischoff, 3).

The principal nerve trunks forming the tympanic plexus are composed of medullated fibres, which run in the periosteum covering the lower and inner walls of the tympanic cavity. They give off small branches to the upper wall, which lie in the stratum of connective tissue subjacent to the epithelium, where they form by their intercommunication a wide irregular network. Non-medullated fibres proceed from this last, which form a delicate plexus immediately beneath the epithelium. Ganglion cells of variable diameter, enclosed in capsules, are found either applied to the surface or imbedded in the substance of the principal trunks, as well as of the branches given off from them, and are seen both in their course and at their points of division. They occur either singly or in clusters and groups. In regard to this point I can only corroborate the statements of Pappenheim (32), Kölliker (22) and Krause (23), and maintain the wide distribution of ganglia, in opposition to the observation of E. Bischoff (3), who regarded them as limited to the branches passing from the tympanic nerve to the fenestra ovalis. I may further add, that in the Dog and Cat I have found a few ganglion cells provided with sheaths, lying immediately beneath the epithelium of the mucous membrane where the fine nerve plexuses are situated.

The mucous membrane in the Dog and Cat presents analogous structural characters to that of Man. The epithelium exhibits the same forms, and beneath it there is a fibrous

layer that presents the same relations to the periosteum as those that have been above more minutely detailed. The principal nerve trunks exhibit at certain points deep constrictions, caused by highly refractile bands, whilst at others they form fusiform enlargements. Ganglion cells are distributed, often in considerable numbers, both in and on the trunks. I found such ganglion-bearing trunks lying close beneath the epithelium, where the cells are columnar, and show the forms mentioned above. These columnar cells are prolonged into slender processes that run towards the nerves, and may be traced into their sheaths, but I am unable to give their further relations.

The nerves themselves exhibit remarkable relations in another point of view. I have been able to demonstrate by injection the presence of capillary bloodvessels, which form, both in the nerve sheaths and amongst the nerve fibres themselves, a narrow-meshed basket-like plexus that may also be rendered apparent by the chloride of gold method. If injected preparations, after previous hardening in alcohol, be treated with solution of chloride of gold, a second system of tubes becomes visible under favourable circumstances, which is not filled with the injection. This usually accompanies the nerve sheaths, or even lies in their substance, and is distinguishable from the blood vascular system by the presence of the spheroidal and fusiform enlargements that are characteristic of the lymphatics. I have succeeded in following branches of this system through the nerve sheaths as far as to the nerve fibres, but have been unable to trace their ultimate distribution in the interior of the nerves.

The statements of v. Troeltsch (44), respecting the presence of mucous glands in the tympanic cavity of Man, have up to the present time remained uncorroborated, though I can substantiate their existence in Dogs and Cats, where they form simple follicles lined by columnar epithelium.

As the further relations of the nerves and lymphatics in these animals are precisely similar to those of Man, I need only add a few remarks on the mucous membrane of the bulla ossea. The membrane here alters its characters; the medullated nerve fibres become fewer in number, and ganglion cells

resembling those of the rest of the membrane lining the tympanic cavity are only sparsely scattered, but are invested by sheaths lying immediately beneath the epithelium. If the epithelium be stripped off from the subjacent very thin layer of connective tissue, an adenoid plexus appears, which in certain regions is very compact, though large openings occur between the groups. The openings lead into funnel-shaped or spheroidal cavities, which again intercommunicate by spaces in the tissue, and are finally continuous with tubes of various width. These

Fig. 286.

Fig. 286. Mucous membrane of the bulla ossea of the Dog. Spaces are visible in the tissue, which at *a* and *b* are continuous with lymphatics; *c*, bloodvessels filled with gelatine. The preparation was stained with chloride of gold.

cavities are traversed by a fine plexus, and are lined by a very delicate epithelium. They may either be empty or filled with lymph corpuscles. They almost invariably contain fat drops of various size, which more or less run together. After maceration in a solution of perosmic acid, these last become black, and then sharply define the course of the tubes and the situation of the cavities. I have, however, also seen fat drops in the veins. However full the bloodvessels may become in consequence of injections made from the aorta, the fluid never penetrates into these cavities and tubes. This circumstance, as

well as their form and contents, justifies us in considering that they belong to the lymphatic system.

I have in vain sought, in works devoted to this subject, for any statements relating to the lymphatics of the tympanic cavity. Prussak (37), who investigated the minute anatomy of these parts in the Dog, denied their existence altogether. He maintained that, owing not only to the mode of formation of the numerous large veins from capillary plexuses, but to the direct connections between small arteries and veins, and to the passing away of large veins at various points, the circulation is carried on under a low pressure, and with great rapidity, by no means favouring exsudations which might have been expected to occur on account both of the loose nature of the soft parts separating the bloodvessels from the tympanic cavity, and of the absence of lymphatics. Now, although the arrangements in the blood vascular system of the mucous membrane in the Dog, described by Prussak, may be admitted to exist, we must nevertheless here also seek, in the *presence* of lymphatics, the principal reason for the non-occurrence of such pathological results; and indeed it may easily be demonstrated that the absorbing surface of the lymphatics exceeds collectively that of the bloodvessels. From the position the lymphatics occupy in the above-described system of cavities, immediately beneath the thin elastic, but easily compressible membranes, we may admit in these cases, besides the ordinary causes effecting the movement of the lymph, the frequent alterations of pressure occurring in the tympanic cavity, since these appear, together with the above-given mechanical arrangements of the lymphatic system, to be well adapted to exercise, sometimes a suction power on the contents of the tympanic cavity, and sometimes a pressure forcing them forward. The statements of Voltolini (46), that a small quantity of clear fluid is constantly present in the tympanic cavity of Man, I can only corroborate in the case of the mastoid cells.

Peculiar cells still require to be noticed, which for the most part lie between the bloodvessels and lymphatics of the deepest layers of the periosteum of the bulla ossea, but are also distributed through the more superficial stratum of connective tissue as far as to the epithelium. In the corpuscles themselves may be distinguished a discoid or more spherical or oval body and several processes. The body of the cell usually exhibits a large vesicular nucleus with a distinct nucleolus, or sometimes

several nuclei, each of which may again contain several distinct nucleoli. Amongst the processes there are usually one larger and from two to five smaller ones. The former, after running a variable distance, usually joins with another similar body, or gives off branches that unite with the processes of other cells, and these lead to the formation of plexuses. The smaller processes branch in a tree-like manner, and ultimately run out into fine processes that under favourable circumstances may be seen to join with nucleated cells. Both the body of the cell and the cell processes, but especially the former, appear to be finely striated and invested by a finely granular mass. Whilst those cells provided with a single nucleus resemble in form the ganglion cells of the spinal cord, those which contain several nuclei are very similar to myeloplaxes. If the latter make the multiplication of nuclei highly probable, this will be rendered certain where disk-shaped appear to be converted into globular cell bodies by the multiplication of nuclei.

Before we now leave the tympanic cavity, we may still add a few words respecting the *ossicula*, their connection with one another, and the muscles attached to them. The ossicula are invested with mucous membrane and in adults with a very thin periosteum. Externally they are composed of compact and internally of cancellous tissue. The latter is traversed by numerous bloodvessels, which, passing through the compact layer, communicate with the vessels of the periosteum or of the mucous membrane. In the head and cervix of the malleus, as well as in the body of the incus, the cancellous tissue increases at the expense of the cortical layer; whilst the converse occurs in the long and short processes of the incus and in the manubrium of the malleus. The articulations of the ossicula agree in their structure with other true joints, having capsular ligaments, whilst a layer of hyaline cartilage covers the articular surfaces.

The mode of attachment of the stapes to the fenestra ovalis will be more minutely described when the soft parts of the vestibule are under consideration.

The muscles of the ossicula are transversely striated, and their tendons, where they traverse the interior of the tympanic cavity, are covered by the mucous membrane by which it is

lined. The tensor tympani is connected with the dilatator tubæ, not only by tendinous fasciculi, as Majer (27) asserts, but also by muscular fibres, as I have already had an opportunity of stating. At the point of its attachment to the malleus, cartilage cells may frequently be found imbedded in its tendon.

THE CELLS OF THE MASTOID PROCESS.

The *mastoid cells* are lined by a very thin mucous membrane, which is continued into them from the tympanic cavity, and, speaking generally, preserves the same anatomical characters in both regions. The epithelium is composed of smooth cells presenting the features that have already been described as characterising those of the membrana tympani. Beneath them is a layer of connective tissue, and beneath this again a second layer of connective tissue representing the periosteum, and containing numerous nerves, bloodvessels, and lymphatics. The upper layer of connective tissue frequently projects in the form of membranes at the free borders of the cells, which extend to adjoining bony processes where they are inserted, and owing to which not unfrequently the cavities of two adjoining cells are shut off from each other. In the larger cell cavities these membranes are stretched horizontally, so as to form a kind of tent, by means of trabeculæ proceeding from them. In the trabeculæ of the membranes the peculiar organs with concentric striation, formerly described, occur with great frequency (I have counted as many as seven). They never attain here to the same size as those of the tympanic cavity, but nevertheless present a much greater variety of interesting forms. They vary from the small fusiform variety to the large spheroidal, clavate, and finger-biscuit form. I have repeatedly noticed membranes with their processes and the corpuscles adherent to them in the aditus ad cellulas, and have also seen trabeculæ in direct connection with the processus brevis of the incus.

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II.

THE EUSTACHIAN TUBE.

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THE Eustachian tube of Man and of the various species of animals, is constructed on the same general plan, but in different instances presents minor modifications of structure. And however close may be the resemblance of the tubæ of various animals, the more minute differences in form they present are so characteristic, that a practised observer can tell, from the examination of a transverse section alone, the name of the animal from which it was obtained.

The Eustachian tube, forming a mechanical apparatus, with cartilaginous and muscular tissues entering into its composition, obviously stands in intimate physiological relation with the tympanic cavity. In addition to the office of carrying off its own secretion and that of the highly vascular mucous membrane of the tympanum, it is capable of effecting, in consequence of its peculiar mechanism, the ventilation of this cavity. Whether the Eustachian tube plays any important physiological part in the conduction of sound into the tympanic cavity, and whether it possesses any relations to the voice of the individual, and if any, what kind of relation, are questions that receive no satisfactory elucidation from researches in comparative anatomy. Conclusive responses to such inquiries have still to be obtained from experimental investigations.

1. Osseous and Cartilaginous portions of the Eustachian Tube.

The *osseous portion of the Eustachian tube* of Man forms an elongated triangular fissure, the greatest diameter of which is almost vertical. The base of the triangle is above, and is bounded by the thin bony lamella which sometimes completely separates the Eustachian tube from the rounded semi-canal of the tensor tympani. If the bony lamella happens to be broad, it curves somewhat upwards anteriorly, in consequence of which the upper end of the tube is of smaller diameter, and comes to occupy a position anterior to the bony semi-canal. As the bony end of the median tubal opening appears dentated and obliquely cut at its point of junction with the cartilage, it is more largely bounded by osseous substance mesially and posteriorly than anteriorly and laterally, an arrangement which, as Henle has already remarked, is deserving of notice, to enable us to understand the mode of attachment of the cartilage to the bone.

If a temporal bone, in which the connection with the Eustachian tube is preserved uninjured, be carefully deprived of its salts, and then be divided through the middle of the tympanic cavity, so that successive sections may be made towards the Eustachian tube, dividing this at right angles, the gradual transition of the tympanic cavity into the bony portion of the tuba, and the relations of this to the cartilaginous portion, may be clearly seen, each section aiding the observer to understand the succeeding one.

By this means it may be shown that the cartilage of the Eustachian tube interdigitates with the dentated margin of the bony portion, and is a direct continuation of the walls of the osseous tuba Eustachii, yet in such a mode, that the hyaline cartilage substance does not immediately succeed to the bone, but that a connection is established between the two by means of fibro-cartilaginous tissue. This is prolonged for some distance into the substance of the cartilage, so that C. F. Th. Krause arrived at the conclusion that the upper end of the Eustachian tube was composed of fibro-cartilage; and it

must be admitted that the two kinds of tissue at this point are not very sharply differentiated from each other, since the basilar fibro-cartilage is partially continued into the Eustachian cartilage.

The cartilage close to the bony portion of the tube presents the form of a lamina, bent at right angles, with a horizontal

Fig. 287.

Fig. 287. Transverse section of the Eustachian tube and the adjoining parts. 1, Median plate of the cartilage; 2, lateral hook of the cartilage; 3, dilatator muscle of the tube; 4, levator palati; 5, basilar fibro-cartilage; 6 and 7, acinous glands; 8, layer of fat on the lateral wall; 9, safety tube (Sicherheitsröhre); 10, accessory fissure (Hilfsspalte); 11, fold of the mucous membrane; 12, tissue bounding the tube laterally.

and a gradually attenuating vertical and lateral limb. No cartilage is as yet present on the median side, because the median and posterior wall of the osseous tuba is longer than the lateral, and therefore here forms its boundary, whilst the opposite part of the wall is already composed of the lateral cartilaginous lamina.

It further appears from such transverse sections, that the transition of the osseous into the cartilaginous tuba Eustachii is very gradual. Cartilage cells appear in the dense fibrous tissue at some distance from the bony tube, at first scattered, but subsequently in larger numbers. The curved hook-like portion of cartilage of the Eustachian tube in Man, which is attached by means of the so-called fibro-cartilago basilaris to the base of the skull, is of moderate thickness, and consists of non-vascular cartilage, which, as Kölliker states, belongs to the same series of structures as hyaline cartilage. Its hyaline matrix, containing a few fibres, includes isolated groups of rounded and oval cartilage cells, of various size. The larger cells contain two or more nuclei, the smaller cells only one. Near the surface the cells become gradually smaller, and there is here a layer of nucleated connective tissue, which represents a perichondrium. No well-defined line exists between the perichondrium and the proper substance of the cartilage, but the one kind of tissue runs gradually into the other. At a few points this vascular tissue dips more or less deeply into the cartilage, so as to form little islands in transverse section, which include, in the Ox, small acinous glands. The fibrous layer is much more strongly developed at the lateral truncated extremity of the cartilaginous hook than elsewhere, which is partly caused by the attachment of the tendon of the musculus dilatator tubæ to it.

In the Quadrumana, as well as in Cheiroptera, the cartilage of the Eustachian tube is hyaline, and very similar to that of Man, the fibrous substance, especially in Bats, being almost suppressed, whilst the hyaline cartilage, containing moderately large cells, greatly preponderates. The same remarks apply to the Eustachian tube of Rodentia, Pachydermata, and Ruminants. In the latter the cartilage cells are small, and the whole cartilage appears to be composed of several segments.

Remarkable differences occur in the external form of the cartilage in different animals. In Talpa Europæa, Arctomys marmota, Canis vulgaris, Mustela martes, and Lutra, there is a simple lamella or cylindrical rod of cartilage on the median side of the tuba, which in Lutra contains a considerable amount of *calcareous deposit*. In the Dog, Marten, and Otter, the

tissue surrounding the cartilage consists of alternate layers of connective tissue and elastic fibres. In Felis domestica, Felis leo, and Felis tigris, the cartilage is essentially limited to a hook at the end of the tubal fissure. The remaining portion of the tuba of these animals is enclosed by dense fibrous tissue, containing small lamellæ of cartilage on its median side.

I once saw a large amount of fat infiltrated into the tubal cartilage of Man, conferring an unusual appearance upon it, by rendering it two or three times larger than natural in all its dimensions; both cartilages projected to a considerable extent from the wall of the pharynx.

2. The Muscular (Membranous) Segment.

I have already had an opportunity of remarking that the expression, "membranous portion of the tube," is very indeterminate. It immediately suggests the mucous membrane to the mind, which however by no means belongs to one segment of the Eustachian tube alone, but lines this throughout its whole extent, and is connected both with the cartilage and with the muscles. If the expression is to be used, it should be understood to indicate that part of the tube which is not invested by cartilage, and there is then no objection to its use, since these two parts can be demonstrated in the Eustachian tube of many animals.

In the meanwhile, though disposed in general to be exceedingly precise in reference to nomenclature, we still think it may be found advantageous for Man and many animals to give up the term at present in use, and to name the segment of the tuba in question the "*muscular segment*."

I am well aware that muscles are here present which do not exclusively belong to the tuba, and that this term does not express the complete morphological characters of the segment of the Eustachian tube in question. No absolute necessity, however, exists that all the characteristic features should be expressed in the nomenclature, and it appears to me that it will be convenient to derive the name of this segment from the muscles which both morphologically and physiologically stand in such intimate relation with it.

As I regard the layer of tissue between the muscles and the mucous membrane as the submucosa, only a few points require to be mentioned respecting the histology of the muscular segment. If it be desired to obtain a general view of the relations of the voluntary musculus dilatator tubæ to the cartilage, transverse sections must be carried through the tuba with its decalcified osseous investment in such a manner that the sections run parallel to the muscular fibres. It may be incontestably shown from an examination of such sections, which ought to be rather thick, that the musculus dilatator tubæ is attached exclusively to the truncated extremity of the lateral cartilaginous lamina along the whole length of the Eustachian tube. (See fig. 287.) Its flat tendon limits the submucosa in the tuba of Man, receives transversely striated muscular fibres on its outer side, and coalesces above with the perichondrium of the uncinate extremity. There can be no doubt that in Man the dilatator tubæ exhibits no direct transition into the mucous membrane. Even in those cases where it appears as though in the vicinity of the cartilage the muscle is continuous with the mucous membrane, sections demonstrate that an isolated fragment of cartilage is connected with the apex of the hook by means of dense tissue.

I am able from transverse sections and surface views to corroborate the statement made by v. Troeltsch and L. Mayer, that a direct passage of the musculus dilatator tubæ takes place into the tensor tympani, and this is true not only in regard to the tendons, but also for the transversely striated fibres of the two muscles. In Monkeys the muscular segment of the tuba, and especially the musculus dilatator tubæ, which is attached exclusively to the truncated extremity of the lateral cartilage, are strongly developed. I have also decalcified the cranial bones of Monkeys, and made transverse sections through the tubæ and their investment, and have found that the musculus dilatator tubæ does not extend beyond the limits of the lateral cartilage. The muscle holds similar relations to the cartilage in the Pig, Horse, Stag, Reindeer, etc. An exception to this disposition of parts however occurs in those animals in which no lateral cartilage of the tuba exists, as in the Marmot, Dog, Marten, Otter, and Cat; in these animals the dilatator tubæ is

directly continuous with the dense submucous tissue. In the case of the Horse it is to be remarked that *two* voluntary muscles, the so-called levator and tensor palatini, are inserted into the lateral part of the cartilage.*

The *musculus levator veli palatini* has a peculiar topographical relation to the Eustachian tube, as it ascends from the bottom of the tubal fissure in immediate contact with the mucous membrane, as far as to the pars petrosa, where it is attached, not only to the bones, but also, with a few fibres, to the dense submucosa of the mucous membrane. A special transversely striated muscle, which is situated on the median side of the Eustachian tube, occurs in the Stag. It is strongly developed in the Buck, its several fasciculi, surrounded by fat, extending to the median portion of the mucous membrane, with which they are intimately connected, whilst its tendon is continued directly into the fibrous layer of the submucosa. It is destined for the fixation of that part of the mucous membrane which is free from cartilage, and I have named it the dilatator tubæ medialis.†

3. The Mucous Membrane.

The mucous membrane of the *osseous portion of the Eustachian tube*, which dips to a variable depth into the inequalities of the osseous surface, varies in diameter between 0·080 and 0·112 of a millimeter. Transverse sections of the osseous portion of the tuba exhibit no well-defined line of demarcation between the periosteum and the mucous membrane. A finely fibrous nucleated connective tissue is intimately blended with the osseous tissue, and processes are given off from it which dip into the bone. At a little distance from the bone the connective tissue becomes somewhat looser in texture, and supports a coarsely meshed vascular plexus, the branches of which are distributed, not only to the mucous membrane, but also in the bone. This layer is remarkably thick on the processes of the bone and at the bottom of the osseous portion of the Eustachian

* S. Rüdinger, *Beiträge zur Anatomie und Histologie der Ohrtrompete.*
† S. Rüdinger, *loc. cit.*, figs. 42 and 43.

tube, where trunks of considerable size, which in part run towards the cartilaginous tuba, are met with in transverse section. At a few points the basement membrane, with its ciliated epithelium, is in contact with the loose submucosa; at other points of the mucous membrane, and most frequently beneath the osseous lamella which divides the Eustachian

Fig. 288.

Fig. 288. Transverse section of the osseous portion of the Eustachian tube. 1, Laminated ciliated epithelium; 2, conglobate gland tissue; 3, periosteum; 4, bone. Magnified 184 diameters.

tube from the semicanalis tensoris tympani, lymph corpuscles occur, closely aggregated in a fibrous reticulum, and we have here that layer of tissue under inspection which has been described under the term conglobate gland substance in the pharynx and in the intestinal canal. It forms a layer, the thickness of which varies from 0·056 to 0·040 of a millimeter, and to it is applied the basal membrane with the ciliated epithelium. (See fig. 288.) This has a thickness of 0·028 of a millimeter.

The pale thin-walled vessels have still to be mentioned, which traverse the submucosa in a plexiform manner, and in transverse sections of injected specimens never contain any of the injection, on which account they have been regarded as lymphatics. All other large spaces and fissures which intercommunicate with one another in the submucosa appear in such injected specimens as blood-conveying vessels. At the

bottom of the osseous portion of the tube, as I have already elsewhere had an opportunity of describing, delicate folds appear of various height, which, when seen in transverse section, present the form of villous processes.

In the *cartilaginous portion* of the tube, the mucous mem-

Fig. 289.

Fig. 289. Transverse section of the Eustachian tube of Man, in its upper third. 1, Median cartilage; 2, lateral cartilaginous hook; 3, perichondrium; 4, submucous layer; 5 attachment of the dilatator tubæ; 6, safety tube (Sicherheits-röhre); 7, lateral projection of the mucous membrane; 8, median projection of the mucous membrane; 9, accessory fissure (Hilfs-spalte). Magnified 184 diameters.

brane and the cavity it encloses present many points of difference from that of the osseous portion, since in it acinous mucous glands and peculiar foldings occur, which are intimately connected with the mechanism of the tube.

In the adult Man I have distinguished two divisions in the tubal fissure. I have applied the term "safety tube" (Sicher-

heits-röhre) to the semi-cylindrical space beneath the cartilaginous hook, and the fissure connected therewith I have called the "accessory" or "auxiliary fissure" (Hilfs-spalte). These two names sufficiently express their physiological significance.

The two divisions are caused by the peculiar configuration

Fig. 290.

Fig. 290. Transverse section of the Eustachian tube of Man, through its upper third. 1, 2, Cartilage ; 3, musculus dilatator tubæ ; 4, lateral submucous layer ; 5, median projection of the mucous membrane, with its vessels ; 6, lateral projection of the mucous membrane, with its vessels ; 7, large vessel on the roof of the tuba ; 8, safety tube, with the mucous membrane ; 9, accessory tube. Magnified 184 diameters.

of the cartilage, and are separated from each other by projections of the mucous membrane. Whilst the mucous membrane at the concavity of the hook behaves itself, in all essential respects, like that of pneumatic canals generally,— that is to say, it is closely adherent to the surrounding parts, and is

only folded at certain definite points,—at that part where the auxiliary fissure commences, folds of the membrane project between it and the safety tube, which present individual variations both in form and size. In the greater number of cases the lateral fold is stronger than the median; but the opposite

Fig. 291.

Fig. 291. Transverse section from the middle third of the Eustachian tube of Man. 1, 2, Cartilage; 3, musculus dilatator tubæ; 4, mucous membrane in folds beneath the hook of the cartilage; 5, slightly elevated mucous folds of the accessory fissure; 6, submucosa.

condition may also be met with, and so far as regards these folds *they are incapable of effecting the complete closure* of the safety tube. This first becomes possible at that part where the curvature of the uncinate process becomes sharp, and the mucous membrane is no longer so intimately connected with the cartilage. This point is situated at about the middle of the length of the Eustachian tube; here the mucous membrane

has a slightly wavy character, as is shown in fig. 291. The configuration of the cartilage at this part renders it possible for the surfaces of the mucous membranes to be immediately applied to one another without any special apparatus, when the cartilaginous lamellæ, owing to their elasticity and the relaxation of the muscles, are approximated. In reference to this point it is to be observed that where a fissure is visible in the middle portions of the tube with high magnifying powers, this is to be clearly distinguished from the oval or semi-cylindrical openings which appear in transverse sections through the upper third beneath the uncinate process of the cartilage.

The safety tube is well marked in the Cat tribe and in the Horse, Roedeer, Sheep, Goat, Calf, Ox, Rabbit, and Hare. On the other hand, it does not present this form in Monkeys, Marmots, Dogs, Martens, Pigs, and Otters.

In the Sheep, Stag, Goat, and Calf, there is a delicate series of folds of the mucous membrane on the concavity of the cartilage, which I described in 1867 and 1868. It does not extend, however, through the whole length of the tube, but is limited to the upper part. The folds are most numerous in the Sheep, Goat, and Calf, whilst in the Ox they have coalesced to form a single projection.

In the Calf the greatest projection measures from base to apex 0·042—0·064 of a millimeter; and in the Ox, 0·080—0·096 of a millimeter. From these measurements, then, it appears that the same structure presents considerable differences in relation to the age of the animal, and it is highly probable that the presence of folds at the concavity of the cartilage is intended to facilitate its movements. At the same time we may reasonably admit that they never attain the same size during life as they present in the dead subject.

In the accessory fissure, where the surfaces of the mucous membrane, when the muscles are not acting, come into contact, numerous regularly opposed folds occur in the pharyngeal segment of the Eustachian tube, which have already been described as they appear in Man by Huschke and F. Arnold. These are also connected with the mechanism of the tuba; for they are most numerous at that part where the median lamella of cartilage attains its greatest amount of mobility.

They occur with more or less modification in the greater number of animals examined, attaining their highest development in the Eustachian tube of the Marmot and Otter, in which only a single sinuous fissure, without any safety tube, is present.

Fig. 292.

Fig. 292. Transverse section of the cartilaginous portion of the Eustachian tube of the Ox. 1, Median lamella of cartilage; 2, mesially directed long process; 3, uncinate process of cartilage; 4, lateral extremity of the cartilage; 5, musculus dilatator tubæ; 6, safety tube, with the fold of the mucous membrane; 7, dilated portion of the Eustachian tube at the commencement of the accessory fissure; 8, accessory fissure. Magnified 184 diameters.

The Eustachian tube of the Bat and of the Horse presents a peculiar structure, the mucous membrane forming a lateral dilatation like an air sac, which is surrounded by muscles and glands. (See fig. 294.)

In the Bat this sac is of an elongated quadrangular form, owing to the disposition of the glands and muscles in relation with it externally.

In the Horse, the wide safety tube is separated from the accessory fissure by a thick process of the mucous membrane. The latter opens into the air sac. This stretches throughout almost the whole length of the Eustachian tube, and the air

Fig. 293.

Fig. 293. Mucous membrane of the accessory fissure of Man, showing the parietal folds and glands. 1, Prominent folds of the mucous membrane, with an epithelium and a subjacent fibrous layer, which last contains many nuclei; 2, submucous fibrous layer; 3, acinous glands; 4, excretory ducts of the glands, lined by transitional epithelium; 5, ciliated epithelium on the lateral wall.

sacs of the two tubes reach to the middle line in front of the vertebral column, and are bounded by the base of the skull and the transverse processes of the two first cervical vertebræ.

The histological characters of the mucous membrane are as follows: Its internal surface is lined throughout by a laminated ciliated epithelium, which has an average diameter of 0·020 of a millimeter. In this, as well as in the osseous portion of the tube, two kinds of cells may be distinguished: (1) Those

Fig. 294.

Fig. 294. Transverse section of the Eustachian tube of Vespertilio murinus. 1, Median cartilaginous lamina; 2, thinner uncinate process; 3, oval-shaped safety tube; 4, auxiliary fissure; 5, elongated quadrangular air sac; 6, musculus levator veli palatini; 7, thick glandular layer; 8, excretory duct of a gland.

which stand in close order on the free surface, and which when they possess cilia are broad, and dip with their attenuated extremities (2) into the deeper layer of cells. The cells forming the latter layer rest by a broad base on the basement membrane, and s nd their attenuated extremities between the cells of the superficial layer. The nuclei of the former are elongated, those of the latter more spheroidal, as well as smaller

and more gelatinous. F. E. Schulze has also described cup-cells in the epithelium of the Eustachian tube, and on examining my finest sections with a view of discovering these cells, I observe between the columnar cells, and situated at definite distances from one another, moderately wide spaces, a disposition that approximatively coincides with that described and pictured as cup-cells. Subjacent to the epithelium and the basement membrane is a fibrous layer, containing numerous nuclei, and presenting different characters in the osseous and cartilaginous tuba. The layer of connective tissue corresponding to the cartilaginous portion of the Eustachian tube, is developed inversely to the glandular layer; where the glandular tissue is thick, as in the neighbourhood of the tubal fissure, this fibrous layer is thin; but where the glands are entirely absent, as in the safety tube, the fibrous layer attains its maximum. A dense layer of connective tissue of considerable thickness makes its appearance above, in the bony tuba beneath the lateral portion of the cartilage, and here the tendinous fibres of the musculus dilatator tubæ are partially interwoven with it. At this part, dense connective tissue is also present at the bottom of the tubal fissure, partly produced by the tendinous fibres of the levator palati muscle. It may be said that the upper end of the Eustachian tube receives from this dense tissue a compact investment in addition to the above-described bone and rectangular plate of cartilage, on which the muscles can exert but a very small influence. If the transverse section be made somewhat lower down, a sharp line of demarcation becomes apparent between the flat tendons of the dilatator tubæ and the submucous connective tissue, and still deeper is a layer of fat.

Mucous glands are entirely absent in the membrane of the safety tube throughout the whole length of the Eustachian tube. In the middle segment of the tubal fissure the acinous glands form a distinct layer, becoming thicker inferiorly between the median cartilaginous lamella and the superimposed mucous membrane. Gland vesicles also occur laterally between the dilatator tubæ and the epithelium, and extend at some points as far as to the truncated extremity of the lateral cartilage. The mucous glands are similar in structure to those of

the pharynx and œsophagus; the several acini become aggregated into larger masses, the moderately wide excretory tubes of which open into the tuba at various points. The epithelium of the ducts presents the characters of a transitional form between that of the mucous membrane and that of the gland

Fig. 295.

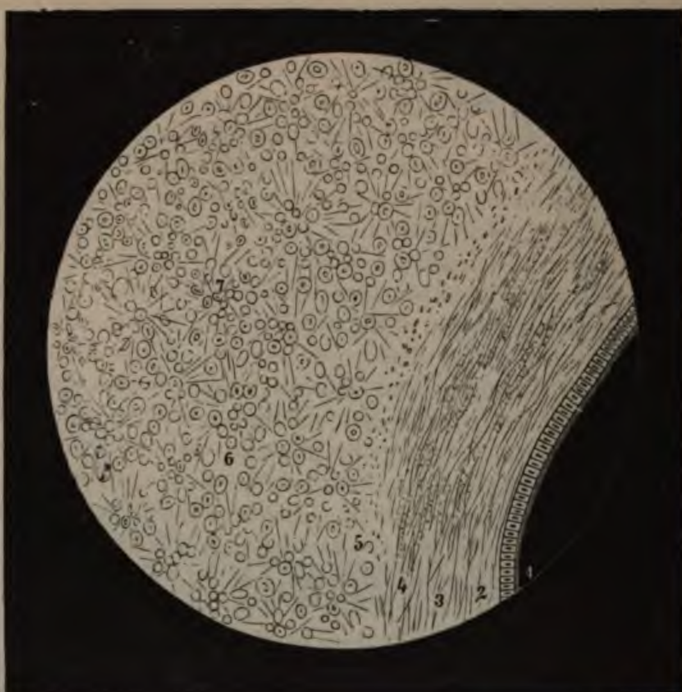

Fig. 295. The cartilage represented in connection with the mucous membrane of the safety tube. 1, Ciliated epithelium; 2, submucosa; 3, dense fibrous layer; 4, perichondrium; 5, cartilage cells with small elongated nuclei; 6, groups of fibres with cartilage cells. Magnified 170 diameters.

vesicles. The several spheroidal or elongated acini are filled by cuneiform epithelial cells, which leave only a small cavity in the centre.

The acinous mucous glands exhibit great variations in their

size and number in the different classes of animals. Whilst in the Quadrumana, in Bats and Marmots, and in the Sheep and Goat, they form a thick layer either limited to certain spots or completely invest the tuba on its central and median side, they appear to be reduced in all the other animals I have examined to a thin layer in the submucous layer. The only histological difference I have been able to distinguish between them is in regard to their size.

4. Nerves.

I have already described ganglion cells as occurring in the nerves of the mucous glands of the Eustachian tube of Man. The nerve fasciculi consist of double-contoured fibres, and originate in the plexus tympanicus and the plexus pharyngeus, forming a coarse network which contains a variable number of ganglion cells at those points where the fasciculi meet. The cells vary in size, and their processes are continuous with primitive fibres. The ganglia agree with those that occur in the branches of the plexus promontorii (E. Bischoff); and since the nerves of the Eustachian tube essentially originate in this plexus, while they also contain sympathetic nerves, we cannot well deny their morphological relation to the tympanic plexus, although their possible functional importance in regard to the mucous glands is on this account by no means excluded.

5. Vessels.

The vessels of the Eustachian tube arise from two different sources; namely, from the vessels of the tympanic cavity, and from those supplying the wall of the pharynx: the latter present no peculiar features in their arrangement, but agree in their characters with the pharyngeal vessels.

The former, on the other hand, run in the first place as large arterial trunks in the direction of the long axis of the tube, both upon its lower part and upon the safety tube, and in transverse sections constantly appear at certain definite points. Thus, in the processes of the mucous membrane situated between the safety tube and the accessory fissure, two vessels of different size become apparent, of which one arises upon

the lateral, the other upon the median side, forming capillary plexuses that do not astomose with the plexus of a third in the middle third of the safety tube. (See fig 290.) This third vessel forms a distinct capillary network in the submucosa, which is extended over the roof of the tuba for a definite distance only.

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III.

THE MEMBRANOUS LABYRINTH.

By PROFESSOR RÜDINGER,
OF MUNICH.

1. Topological and Histological Account.

In consequence of experimental observations, some doubt has been thrown on the functional importance of the membranous labyrinth for the faculty of hearing; it must still, however, be considered an integral part of the inner ear, by virtue of its being the supporter of the acoustic percipient apparatus. Its topographico-histological relations present numerous differences in the various classes of animals. In many Invertebrata, as in Mollusca and Crustacea, a vesicular structure appears as the representative of the labyrinth, which is usually seated on the nerve centre, or on one of its branches. In the Achetidæ and Locustidæ, amongst Insecta, it is placed near the knee-joint; and in the Acrididæ, over the origin of the last pair of feet. In almost all Vertebrata the *membranous labyrinth* forms a division of the auditory apparatus, that is found to be enclosed more or less completely in a cartilaginous or osseous capsule, of which it forms an attenuated protrusion. The elongated sac, or *utricle*, with its ampullæ and semicircular passages, as well as the more rounded *sacculus*, are in direct contact with the osseous or cartilaginous capsule, and are not, as has hitherto been erroneously believed, completely surrounded by fluid (perilymph).

These topographical relations of the labyrinth are already

recognizable in the embryo.* Sections made through the temporal bone at various stages of development show that the cavity of the vestibule and of the semicircular canals is filled with a gelatinous substance, which becomes con-

Fig. 296.

Fig. 296. Membranous labyrinths of various vertebrate animals. *A*, from Man; *B*, from the Calf; *C*, from the Pike; *D*, from Vultur fulvus; *E*, from Rana esculenta. 1, Canalis semicircularis horizontalis; 2, can. sem. superior; 3, can. sem. posterior; 4, canalis communis; 5, ampulla-form termination of the can. sem. horizontalis; 6, utriculus; 7, sacculus rotundus.

densed near the cartilaginous wall, and that the parts of the labyrinth are connected with this somewhat denser fibrous layer. The vessels that develop in this part traverse the

* Kölliker first gave an illustration of the relations of the semicircular canals in the fœtus, in his *Entwicklungsgeschichte*, or *History of Development*.

gelatinous tissue in such a manner that the larger branches appear in sections made in the direction of the long axis of a semicircular canal, whilst the secondary branches run in a more or less transverse or oblique direction. Of the two larger vessels (see fig. 297) which constantly run with some interval between them, I regard the smaller as the artery and the larger as the vein. In the formation of the cavities or lumina of the tubes, the periosteum and the nucleated connective tissue surrounding the vessels which traverse the cavity, may be regarded as the results of the regressive metamorphosis

Fig. 297.

Fig. 297. Transverse section of a cartilaginous and membranous semicircular canal of a fœtus. 1, Cartilaginous semicircular canal; 2, gelatinous tissue, which completely fills the space between the two canals; 3, vein; 4, artery; 5, wall of the membranous semicircular canal.

of the gelatinous tissue, and as constituting the ultimate products of its development.

In the *adult human subject* the *periosteum* lining the osseous labyrinth is a moderately thick layer of connective tissue intermingled with fine elastic fibres. Both it and the vessels it encloses are continuous with those of the bone, so that it is difficult to detach it from the bone. The internal surface of the periosteum in the semicircular canals is uneven. Rather large nuclei are scattered through its substance, which become more numerous, and are less regularly arranged, near the free than

the attached surface. In specimens that have been hardened in chromic acid or in chromate of ammonia, these nuclei sometimes form regular rows, so as to present many of the characteristic appearances of a pavement epithelium. After repeated observations recently made on carefully prepared specimens, I am inclined to think that, as Henle and Hasse have already stated, there is really no epithelium here, but that the appearances presented are simply due to the numerous nuclei of the periosteum. Henle finds the periosteum of the labyrinth analogous to the sub-arachnoideal tissue, the pigment cells, however, being very few in number. The calcareous particles described by Kölliker and Henle as existing in the periosteum are absent in some cases, whilst in others they are very numerous.

If an attempt be made with the aid of a chisel to dissect out the labyrinth, it will soon be discovered that not only the two sacculi in the vestibule, but also the membranous semicircular canals, are at certain points closely connected with the periosteum. A clear view of the histological relations of the osseous and of the membranous labyrinths respectively, can therefore only be obtained by making transverse sections through the temporal bone decalcified in chromic acid.

In reference to the sacculi it may be observed that the utriculus is more closely attached to the bones of the median wall of the vestibule, than the sacculus rotundus. This, as Odenius has already pointed out, is separated from the recessus hemisphericus by a moderately thick and loose layer of connective tissue, which surrounds the nerve fibres and vessels traversing it. The two sacculi occupy about two-thirds of the cavity of the vestibule. The utriculus extends farther laterally than the sacculus rotundus, but neither of the two touches the lateral wall of the vestibule or footplate of the stapes; topographical relations that I had already described in 1866.*

The membranous semicircular canals are attached to the periosteum on the convex side of the osseous canals by moderately broad bands of connective tissue, which I call the *ligamenta labyrinthi canaliculorum et sacculorum.* At the points

* *Aerztliches Intelligenzblatt, Juni.*

where the membranous canals adhere to the bones, the periosteum is feebly developed; in the angular spaces, on the other hand, where the canals separate from the bones, strong nucleated fasciculi of connective tissue pass from the periosteum to the external fibrous layer of the membranous semicircular canals, and these ligamenta labyrinthi canaliculorum form the *essential means by which the semicircular canals are retained in position.* In some cases there are two or more bands

Fig. 298.

Fig. 298. Utriculus and sacculus rotundus, drawn with the camera lucida. 1, Utriculus; 2, sacculus rotundus; 3, macula acustica; 4, ampulla; 5, canalis communis.

which enclose variously shaped spaces between them. These spaces appear to be the transverse sections of small canals which run along the ligaments to the principal membranous canal. They may even be found in the neighbourhood of the ampullæ, but I do not think that any particular morphological or physiological importance is to be attributed to them. In the sacculi and ampullæ, these ligaments, or rather

means of fixation, are feebly developed in those angles where the former separate from the bones. Vessels are constantly met with in transverse sections of the ligaments.

The moderately tense and finely fibrous fasciculi of connective tissue traversing the cavity of a semicircular canal (see fig.

Fig. 299.

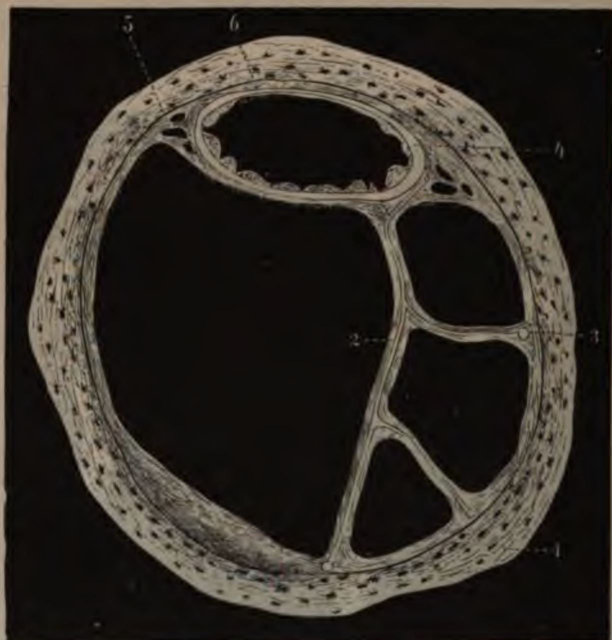

Fig. 299. Transverse section of an osseous and membranous semicircular canal of Man. 1, Osseous wall; 2, fasciculi of connective tissue, with vessels enclosed within them; 3, point of junction of the fasciculus with the periosteum; 4, membranous semicircular canal, with its three layers; 5, ligamenta canaliculorum, with their spaces or cavities; 6, point where the membranous semicircular canal coalesces with the periosteum.

299), which are attached on the one hand to the periosteum, and on the other to the free wall of the labyrinth, are to be regarded as essentially the carriers of vessels, and also as means of fixation for the *free wall* of the membranous semicircular canal. They for the most part run at right angles to the longitudinal

axis of the semicircular canals, give off secondary branches to the periosteum, and are attached to the most diverse points by their gradually expanding extremities. The two sacculi are attached in a very similar manner, except that the finely fibrous connective tissue (the *ligamenta labyrinthi sacculorum*) is much more feebly developed at those angles where the sacculi separate from the bone. In the *Quadrumana* and *other Mammals*, the labyrinth, which upon the whole is very thin-walled, appears to be as firmly attached as in Man. The connection with the periosteum and the vessels with their

Fig. 300.

Fig. 300. Transverse section of an osseous and membranous semicircular canal of a Rat. 1, Osseous semicircular canal; 2, plexiform fibrous tissue; 3, wall of the membranous semicircular canal; 4, connective-tissue corpuscles; 5, pigment cells.

delicate investing tissue, is only so far different that the ligamenta labyrinthi canaliculorum appear to be less sharply defined. In the Rat the interior of the osseous canals is everywhere traversed by plexiform bands of connective tissue and scattered pigment cells, and is quite half filled by the membranous excentric membranous canal, so that here there is quite a different proportion in point of size between the osseous and membranous canals to that observed in Man. No difference

exists in the mode of attachment to the bone of the two vestibular sacculi.

In the osseous semicircular canals of Birds, according to Hasse's and my own observations, the position of the utriculus and of the membranous semicircular canals is also excentric. The membranous ampullæ, on the other hand, certainly appear to be the outlets of the osseous canals, being in contact with the periosteum of the bone throughout their whole extent. The membranous canals are applied to the periosteum of the convex side of the osseous canals, though they do not

Fig. 301.

Fig. 301. Transverse section of an osseous and membranous semicircular canal from the Goose. 1, Superior osseous semicircular canal; 2, connecting fibres stretching from the periosteum to the membranous semicircular canal; 3, membranous semicircular canal with epithelial lining; 4, attachment of the thinner part of the membranous semicircular canal to the periosteum.

appear to be imbedded in the periosteum in the manner I have described above as occurring in Man. Their free wall is connected with the rest of the periosteum by means of a fine plexus, and in the Rat, as well as especially in Birds, Fishes, and the Anourous Batrachia, it may be demonstrated that the space which bounds the free surface of the membranous semicircular canals and the utriculus is not enclosed by any serous layer lined by epithelium.

In *Fishes* also the membranous canals are adherent to the

solid wall. The relatively wide cartilaginous or osseous canal is here partially filled by a plexus of broad fibrous trabeculæ, which enclose a system of cavities filled with mucus. The rest of the space is occupied by the membranous canal which is loosely adherent to the wall, and by a fine fibrous plexus that does not essentially differ from the above-mentioned gelatinous tissue in the canals of the human fœtus and of the Frog.

In his first communications on the Frog, Hasse made the following statement, that he had observed certain markings on the outer surface of the membranous canals in this animal, which gave the impression of the presence of an epithelial investment. But transverse sections made through the membranous labyrinth whilst still adherent to the bone show histological relations (especially well marked in the osseous semicircular canals) which thoroughly negative the existence of a serous layer; for if successful sections be examined, we may perceive that the anastomosing connective-tissue corpuscles which completely fill the canal, and which in the human embryo we have termed gelatinous tissue, are persistent in the Frog. Whether they remain in this condition throughout the whole of life I am unable to say, since my researches have only been made on Frogs at the end of the winter.

In the gelatinous tissue *in the Frog* I find also many large pigment cells, of which a few adhere intimately to the outer side of the membranous canals. A still richer deposit of pigment exists in the neighbourhood of the utriculus and of the otolithic sac in the vestibule, so that the point of entrance of the nerves and vessels into the utricular wall is rendered somewhat obscure. In regard to the support received by the walls of the membranous labyrinth of the Frog, it is to be remarked that the utriculus, the otolithic sac, the ampullæ, and the commencement of the membranous canals lie tolerably close to the dense capsule; but, on the other hand, it cannot be denied that the membranous semicircular canals, where they are most remote from the vestibule, become detached from the wall of the osseous canal, so that they appear to be everywhere surrounded by nucleated finely fibrous connective tissue. Should any one be disposed to regard this as a result of manipulation, he should not forget that the connection between the entire membranous

labyrinth and the periosteum in the Frog is by no means so intimate as in Birds, Mammals, and Man; a relation that may possibly be regarded as dependent upon the degree of regressive metamorphosis undergone by the gelatinous tissue.

2. Wall of the Labyrinth.

The histology of the wall of the labyrinth is most advantageously studied in transverse sections. The semicircular canal, which is oval or transverse in section, appears to be *of unequal*

Fig. 302.

Fig. 302. Transverse section of a membranous semicircular canal from Man. 1, Free portion of the wall, with the fibrous layer and connective-tissue corpuscles; 2, tunica propria; 3, papillæ, with their epithelium; (4, omitted;) 5, portion of the wall free from papillæ, with a thin layer of the tunica propria; 6, strongly developed papillæ at the boundary of the portion destitute of papillæ; 7, ligamenta labyrinthi canaliculorum.

thickness. (See fig. 302.) In the semicircular canals of Man, the thickness of the wall where attached to the bone, exclusive of the periosteum, is 0·016 of a millimeter; the free wall measures 0·028, and at the points where it is fixed by the ligamenta labyrinthi canaliculorum it has a diameter of 0·060—0·080 of a millimeter.

Four layers of tissue may be distinguished in the wall of the

semicircular canals. (1) The layer of connective tissue; (2) the hyaline tunica propria; (3) the papilliform or villus-like processes, and (4) the epithelium.

The *outer fibrous layer* is composed of connective tissue with numerous nuclei scattered through its substance, which for the most part runs circularly around the canal, and presents no particular marks distinguishing it either from the above-described ligaments, or from the periosteum. Where the canal is in contact with the periosteum, the outer fibrous layer is very thin; but it becomes thicker where the wall is free and attains its greatest development; that is to say, at the point where the ligamenta labyrinthi canaliculorum are attached. The large and for the most part rounded nuclei, owing to their mode of arrangement on the outer surface of the free wall of the canal, quite give the appearance of an epithelial investment. The nuclei, however, have a similar disposition in the ligaments of the labyrinth, and on the side of the periosteum; so that in good imbibition preparations it may be clearly seen that the outer surface of the membranous canals are not really invested by a layer of pavement epithelium.*

If an examination be made of the entire semicircular canal which, with the periosteum and the ligaments, has been withdrawn from its natural position, another fibrous plexus comes into view near the vessels, of the nature of which I am still doubtful. The trabeculæ of this plexus are pale and moderately broad, and form regularly arranged meshes. At the nodal points they become much broader, exhibit their fibrous nature more distinctly, and contain large nucleated cells in their substance. At first sight this plexus presents precisely the aspect of nerves with intercalated ganglion cells (fig. 303). Whether they really are nerves or some other kind of tissue, I am unable at present to state with certainty. It need scarcely be remarked that it would prove of great interest if these turned out to be the nerves of the membranous semi-

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* According to Schwalbe and F. E. Weber, the space between the membranous and the osseous labyrinth filled with perilymph is a lymph space, since injections into the cavity of the arachnoid penetrate into it through the porus acusticus.

circular canals, the existence of which has up to the present time been doubted.

In the sacculi the fibrous layer is thin, except where the nerves penetrate the osseous wall. At these points the sacculi are not very intimately connected with the osseous wall (the utriculus, however, more closely than the sacculus rotundus), but are separated from it by a wide-meshed connective tissue enclosing vessels and nerves.

Fig. 303.

Fig. 303. Fibrous network adjoining the vessels of the semicircular canals of Man, with its cells.

The second layer, the vitreous-like *tunica propria*, likewise varies in thickness. At the attached parts of the membranous canals it appears in transverse sections as a very thin layer, which increases in thickness towards the free portion of the wall, and acquires considerable dimensions at the points of attachment of the ligaments of the labyrinth. In fresh specimens it forms a hyaline substance that appears sharply defined both externally towards the fibrous layer, and internally towards the papillæ. After the application of colouring agents

and other tests, it presents the appearance of a granular slightly striated membrane. It is demonstrable in the utriculus, but is there reduced to an extremely thin uniform layer.

The *papilliform processes** on the inner surface of the tunica propria must, in my opinion, be regarded as normal structures in the adult Man. They are so constant that I almost regard their absence as an evidence of disease. They are limited to certain parts of the wall of the canal, on which account I have elsewhere divided this wall into a papillated and a non-papillated portion. They appear as transparent spheroidal structures varying greatly in form and size in surface views of the membranous canals of adults,† and in transverse sections are recognisable as projections. They rest with a broad base upon the tunica propria, and project into the lumen of the canal in the form of small clavate or conical processes.

Towards the tunica propria they have no well-defined line of demarcation, and they must therefore be regarded as constituting integral portions of the membrane; especially as they develop from it, and are completely identical with it in structure. In the embryo, and even in the new-born child, the papillæ are entirely absent, appearing first at a later period on the inner surface of the wall of the canal opposite the points where the ligaments of the labyrinth are attached externally. The thin portions of the wall of the membranous canals which are adherent to the bone are everywhere completely destitute of papillæ. I have never even seen the slightest indication of them at these points, notwithstanding

* I use the above expression instead of villus-like, which I formerly adopted, because the structures in question resemble papillæ rather than villi. Hasse has expressed the opinion that I have mistaken striæ shining through the tissue for papillæ or villi,—a supposition that convinces me that Hasse has never examined the bodies in question in the adult; for to exhibit the papillæ in transverse sections is one of the easiest things possible, and a mistake is impossible.

† Whether the papillæ are identical with the "large spheroids" described by Pappenheim, at pp. 43 and 44 of his treatise devoted to the histology of the auditory organs, I am unable, from the obscurity of his statements, to determine.

that the tunica propria is here present, though certainly only as a very thin layer (see fig. 302). Towards both sides the processes begin to increase in size, and then become (as shown in the figure) larger on the right and left hand; again diminishing in height at the free wall of the labyrinth. At this last-named part they are frequently but little elevated above the free surface, so that on examination with low powers they may appear to be absent. Their internal surface is everywhere covered, as well in the depressions between the papillæ as on

Fig. 304.

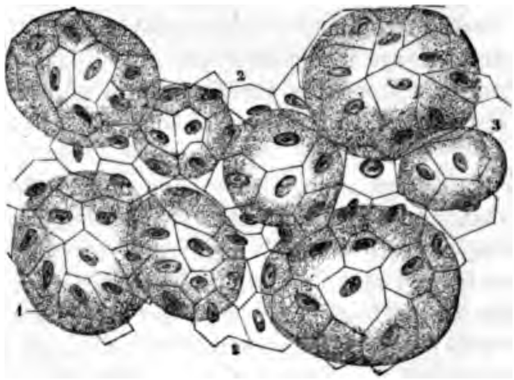

Fig. 304. Surface view of the papillæ of the membranous horizontal semicircular canal (stained with nitrate of silver solution). 1, 2, 3, papilliform structures, with their investing epithelium.

their summits, by a single layer of tesselated epithelium, which may be brought into view without much difficulty with various agents, both in surface and profile views. But since these epithelial cells become rather easily detached, and the smallest papillæ frequently only bear from three to five epithelial cells (see fig. 304), the nuclei of the cells cannot always be seen in profile, which has led to the existence of the epithelial cells on the summit of the papillæ being incorrectly denied (Lucæ). The epithelial cells on the papillæ and neighbouring parts are of irregular form, and by maceration in solution of nitrate of silver their contours can be traced over all parts of the elevation. Inasmuch as these structures first make their appearance after birth, it is probable that during their development

they simply extend in a mechanical way the epithelial cells originally situated at regular and definite distances from each other, which Eberth has shown must be admitted to occur also in many of the separable forms of epithelium lining various vessels, and which holds equally for the vesicles of the lungs, if it be true that they are lined by epithelium in the adult. Although individual peculiarities occur in regard to the papillæ, I have never missed them entirely. At some distance from the thin part of the wall, *i.e.*, the part corresponding to the attachment of the canal ligaments, they are never absent; but on the free side of the canal they are sometimes but feebly developed. They are not found in the sacculus or near the openings of the semicircular canals into the utriculus. I have on several occasions seen isolated papillæ near the dilated orifice of the membranous horizontal canal.

These structures, peculiar to the adult Man, have been regarded as pathological products (Voltolini, Lucæ). Lucæ has stated in favour of his view that they are not present in the newly born child; that they have no epithelium; and that, owing to the reaction with iodine, they may be placed in the same category as the amyloid corpuscles. On the other hand, putting aside the first point as irrelevant, it may be observed (1) that the papillæ in the semicircular canals of adults, though presenting individual variations in regard to the degree of their development, were never found by me to be absent; * and (2) that by means of reagents the epithelium can be demonstrated, whilst the well-known iodine reaction is common to them with the tunica propria and many other tissues in which starch proper still remains to be discovered. The rounded form which the papillæ assume under manipulation cannot certainly be advanced as an argument in favour of their amylaceous character. I have convinced myself, by making very fine transverse sections of the membranous semicircular canals, that the papillæ

* If thirty subjects be taken successively from the dissecting room, without reference to the nature of the previous disease, and an examination be made of their semicircular canals, the papilliform processes will be found in twenty-eight; a numerical proportion which, independently of other grounds, is, *per se*, sufficient to lead us to discard the idea of their being pathological.

are really to be regarded as part of the tunica propria. The line of demarcation which, in transverse sections, occurs between the membrane and the papillæ (fig. 302) depends only upon the thickness of the section. In very fine sections no contour lines are perceptible between the two, even when examined with high powers. If we may assume that the membranous canals secrete the endolymph, it is obvious that the papillæ, quite independently of other physiological functions, constitute structures that effect great extension of the surface.

In Mammals, the walls of the membranous labyrinth are much thinner than in Man. The thickness of their membranous semicircular canals varies only to a slight extent, and the mucous membrane has no papillæ.

In Birds, the membranous labyrinth varies in thickness in the utriculus, the ampullæ, and to a remarkable extent in the semicircular canals. Where the canals, which appear oval on section, are adherent to the osseous wall, they are extremely thin; but the thickness of their wall gradually increases towards the unattached part of their periphery. The thinnest part has a diameter of 0·020, and the thickest of 0·080 of a millimeter. I cannot corroborate the statement of Hasse, that the thickness of the walls varies within small limits, and that *no constant* can be given for particular regions. According to my observation, the thin portion of the wall of the canals is completely limited to the surface attached to the periosteum; whilst the thick portion, which moreover presents a groove for the reception of the larger vascular branches, is turned away from the bone.

The connective tissue present in the osseous canal is the only representative of a fibrous layer on their external surface. The thick tunica propria, which, in conjunction with the epithelium on the basement membrane of the inner surface, forms the wall, has been described in Birds, Fishes, and Reptiles, as the "*Labyrinth Cartilage.*" In the important treatises of Leydig, Deiters, and Hasse, exact descriptions with illustrations will be found of the histology of the wall of the canal. Elongated or polygonal small stellate nuclei are distributed somewhat sparingly through a structureless matrix which only presents a finely granular appearance in specimens that have been pre-

served in chromic acid. Whilst the great majority of the processes of the connective-tissue corpuscles are circularly disposed in the canal, others traverse the thick part of the canal

Fig. 305.

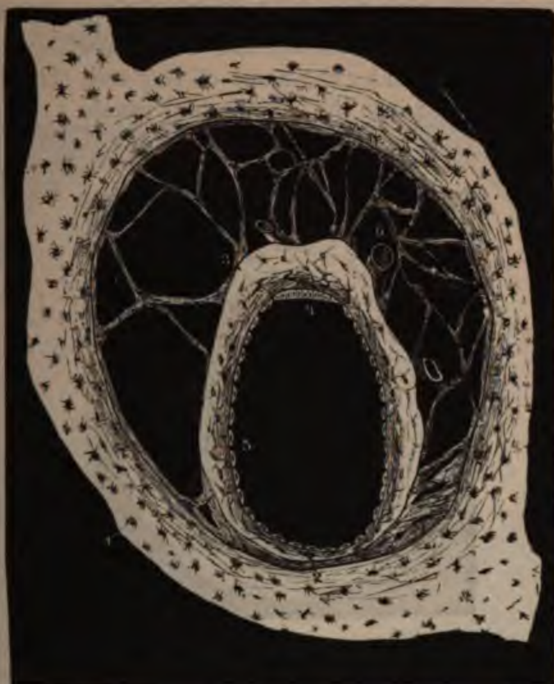

Fig. 305. Transverse section of the sagittal semicircular canal of the Pigeon. 1, Osseous semicircular canal; 2, thin portion of the wall of the membranous canal coalesced with the periosteum; 3, thick portion of the wall, with a groove for an artery; 4, epithelium of a different character from the pavement epithelium; 5, pavement epithelium; 6, plexiform trabeculæ stretching between the periosteum and the outer surface of the membranous semicircular canal. Magnified 170 diameters.

in a direction from without inwards. (See fig. 306.) The coarse vascular networks that surround the membranous canal also partially dip into the cartilage, without however extending as far as the epithelial layer of cells.

These form a regular tesselated epithelium upon the inner surface of the basement membrane on which they rest. A larger form of epithelium occurs on the thicker part of the canal wall; but to a limited extent only; the appearance presented being as though the peculiar columnar epithelial cells of the utriculus and of the ampullæ, which form a narrow stria opposite to the nerve epithelium, and which have been minutely described by Hasse under the name of *roof-cells* (Dach-zellen), were also continued into the semicircular canals.

Fig. 306.

Fig. 306. Sagittal semicircular canal of the Pigeon. 1, Groove on the thick portion of the canal for the reception of a vessel; 2, thinner portion of the wall; 3, cartilage of the labyrinth traversed by large vessels; 4, pavement epithelium. Magnified 170 diameters.

The proportionately thick-walled semicircular canals of the *Fish** vary in their thickness and in the shape of their lumina in the different families. In the Pike (fig. 307) the canal is triangular on transverse section, with a thick basal segment (corresponding to the thick free portion of the wall), and two lateral portions which, gradually becoming thinner, join in an arcuate manner. The part which is adherent to the bony

* My own investigations have been limited to the families of the Perch, Carp, Salmon, and Pike.

or to the cartilaginous canal wall is here also the thinnest having a thickness of 0·080 of a millimeter; whilst that of the thicker part varies from 0·160 to 0·120 of a millimeter. It is composed of a firm hyaline matrix, distributed through which are numerous stellate connective-tissue corpuscles, that form, by the anastomoses of their somewhat granular processes, a coarse plexus, exhibiting on close examination, in the Pike, the arrange-

Fig. 307.

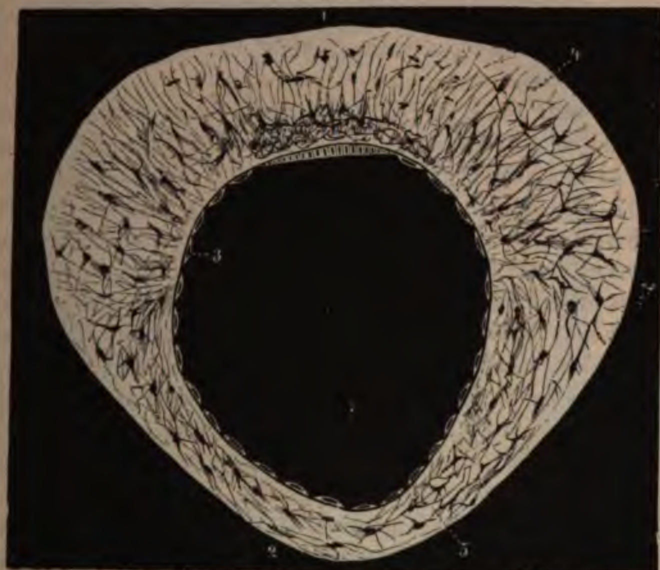

Fig. 307. Transverse section of the membranous semicircular canal of Esox lucius. 1, Thick free portion of the canal; 2, thin supported portion of its wall; 3, tesselated epithelium, becoming columnar on the thick portion of the canal; 4, cartilage of the labyrinth, with radial fibres and connective-tissue corpuscles; 5, circular fibres and connective-tissue corpuscles.

ment displayed in fig. 307. On the thin part of the wall of the canal the fibres run round the lumen of the canal. At the two thickest parts they appear in the form of lines, which traverse the wall in a transverse direction from without inwards. There is no layer of connective tissue on the outer side of the canal; a pavement epithelium rests on the basement

membrane of the inner surface, composed of moderately large cells with well-defined nuclei, which, when seen in profile, are fusiform. In the Pike there is a much broader band than elsewhere, situated on the thick side of the canal, and composed of columnar cells. In no animals do the epithelial cells with their basement membrane separate so easily as in Fishes; the whole lamella becoming detached, and appearing as a smaller canal on transverse section, which may be adherent to some point of the cartilage wall. Frequent examination leads, however, to the conclusion that this is the result of manipulation, and is due to the loose connection of the epithelium with the tunica propria.

In the year 1844, A. Ecker described the presence of ciliated epithelial cells in the semicircular canals of Petromyzon marinus, which, however, as H. Reich, a pupil of Ecker's, observed in 1857, in the Ammocœtes, really belong only to the crista acustica or macula acustica, and not to the semicircular canals.

I have observed a peculiar isolated structure in the membranous labyrinth of *Salmo hucho* (fig. 308). In the adjoining figure it may be seen that the wall and the lumen of the canal in this fish present many points of difference from that of the Pike. The thick portion of the external wall of the canal is unevenly divided by a groove on its external surface, and the hyaline matrix is present in much larger proportion in relation to the connective-tissue corpuscles.

Arising from the thick portion of the wall are *two rows of cells*, with an interval between them. They form, as it were, the two *walls of a groove*, and project to a moderate distance into the canal. (See fig. 308.) These extend along the whole length of the canal, with this difference only, that their height diminishes towards the utriculus.

From beneath the epithelial cells situated at the margin of each wall, very delicate pale fibres project, which are surrounded at their origins by protoplasm, undergo dichotomous division, and are connected with rounded or oval cells like grapes on their stalks. The whole row of cells which is thus formed floats to a certain extent in the endolymph of the semicircular canal. Surface views show that both cell rows extend at definite distances towards each other, so that as it

were they bridge over the furrow. I presume, however, that the two rows are not connected with those of the opposite side by means of their stalklets, but that the cells are only in contact and adherent to each other. If a similar spot be struck in

Fig. 308.

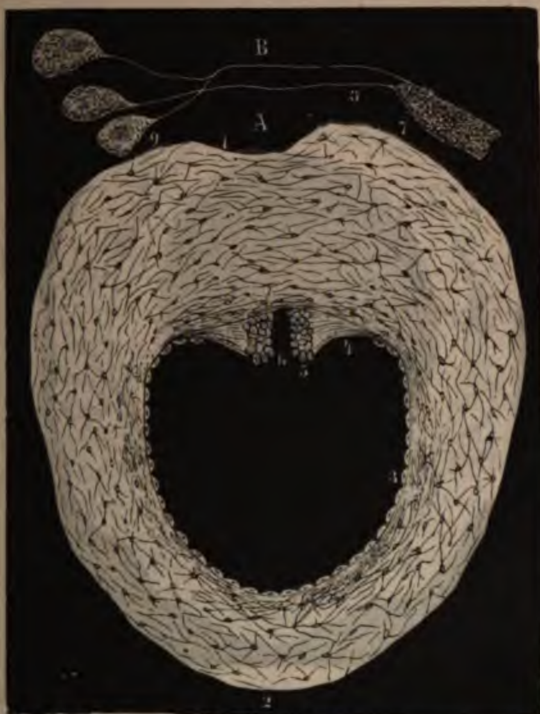

Fig. 308. *A*, Transverse section of the membranous semicircular canal of Salmo hucho. 1, Thick portion of the wall of the canal, with a groove upon its outer surface; 2, thin attached portion of the wall; 3, pavement epithelium; 4, fine fibres proceeding from 5, the series of cells; 6, a furrow between the two rows of cells.

B, Highly magnified fibres and cells, isolated; 7, protoplasm, from which the fibres (8) take origin; 9, cells to which the dividing fibres become attached.

transverse section, the structure in question presents the appearance of a complete canal; and if an attempt be made to move it mechanically under the microscope, it may be seen

that although the cells rise and fall, the two rows do not separate from one another. The furrow between the two walls does not appear to be lined by an epithelium. I do not believe that this constitutes a terminal nerve apparatus, since the

Fig. 309.

Fig. 309. Transverse section of the semicircular canal of the Rana temporaria. 1, Cartilage, with a few connective-tissue corpuscles; 2, fibrous plexus, with connective-tissue corpuscles and pigment cells; 3, pavement epithelium.

branches of the nervus acusticus are not distributed over the ampullæ; and I have not been able to distinguish any primitive nerve fibres external to the wall of the canal. Is it possible that the two walls and the furrow they bound stand in any relation to the undulatory movement of the endolymph?

Amongst *Batrachia* I have only examined the labyrinth of the Frog. The membranous semicircular canals are perfectly circular in section, and the walls are everywhere of uniform

and moderate thickness. Their thickness amounts upon the average to 0·040 of a millimeter. A few oval connective-tissue corpuscles are distributed through the whitish hyaline matrix. On the outer surface there are pale fibres which run through about one half of the thickness of the wall, and as this striation occurs equally in all sections, I cannot regard it as due to the accidental formation of folds. The *interior* is lined by a large-celled pavement epithelium.

3. The Vessels of the Membranous Labyrinth.

The vessels distributed to the sacculi, the membranous semicircular canals, and the periosteum of the labyrinth, differ in their arrangement in these several regions; for whilst at the point of entrance of the nerves into the sacculi and ampullæ there is a very rich and close vascular plexus, the membranous canals are surrounded by a coarse plexus with wide loops.

The larger arteries pass to the walls of the utriculus and sacculus rotundus in company with the branches of the vestibular nerves, and form strong coarse plexuses opposite to the macula and crista acustica in the loose connective tissue between the bones and that part of the wall of the sacculus which bears the macula acustica. On the wall of the sacculus itself the capillaries become finer, and, towards the periphery of the macula, form numerous loops, without however penetrating the substance of the tunica propria. In Birds and Fishes, large capillary loops traverse the tunica propria, and extend to the basement membrane. In Man, fine capillaries reach beyond the limits of the maculæ acusticæ and are distributed in the external fibrous layer of the wall of the sacculus, which is destitute of nerves.

Proceeding from the vestibule, large arterial branches run into the osseous semicircular canals, and pursue an arched course corresponding to the axis of their curvature. The vessels are collectively surrounded and fixed in their position by a relatively thick and nucleated investment, which is a residue of the fœtal gelatinous tissue destined for the attachment of the vessels. From the larger vessels running in the centre of the osseous canals finer but still tolerably thick-walled branches are

given off both towards the periosteum and towards the free wall of the membranous canals and the ligamenta labyrinthi canaliculorum; from whence, surrounded by a few fibres of connective tissue, they return as veins. The arteries and veins do not lie in close contiguity in the osseous canals, and it is frequently very difficult to distinguish them from each other, or from the thick-walled capillaries (fig. 297).

Towards the vestibule the two vessels become approximated, although it is still doubtful whether the veins follow the course of the branches given off by the arteria auditiva interna.

Transverse sections through the aquæductus vestibuli demonstrate that large vessels run close to this serous passage, which, from their external characters, appear to be veins, and which have already been described by Hyrtl as the veins of the vestibule.

4. NERVES AND EPITHELIUM OF THE AMPULLÆ AND SACCULI.

Corresponding with the region of the distribution of the auditory nerve in the sacculi and ampullæ of the various classes of animals, the internal surface constantly presents a peculiar form of epithelium, for the most part containing yellowish pigment, and beset with firm cilia; so that, from the constant coincidence on the opposite sides of the membrane of the above-mentioned morphological elements, we may draw the conclusion that they are necessarily associated together. For the study of the topographical and histological characters of the *nerves* and their relations to the *epithelium* of the ampullæ and sacculi, fresh sections made in various directions through specimens that have been decalcified and hardened in chromic acid, and those also which, after being made, have been allowed to imbibe various fluids, and have been further divided, are best adapted.*

After attention had been directed by Scarpa and E. H. Weber to the mound-like process (called "septum" by Scarpa)

* I find of especial value that mode of imbibition which proceeds under the eye of the observer. To this end I lay transverse sections of the ampullæ with the nerves upon a slide, and add a few drops of perosmic acid, watching at the same time its gradually increasing action on the nerves and epithelium.

in the ampullæ, Steifensand closely studied it, in the year 1835, in Fishes, Reptiles, Birds, Mammals, and Man, and demonstrated that this process, varying in its form in different animals, is produced by a peculiar inversion and thickening of

Fig. 310.

Fig. 310. Transverse section of the ampulla of the Pike. 1, Roof of the ampulla; 2, thin portion of the lateral wall; 3, thick portion of the lateral wall; 4, 5, 6, floor of the ampulla, with the nerves; 7, nerve epithelium; 8, auditory hairs; 9, transitional region between the floor of the ampulla, and 10, the planum semilunare; 11, pavement epithelium.

the wall of the ampulla. M. Schultze applied to the septa the certainly more accurate name of cristæ acusticæ in the ampullæ, and maculæ acusticæ in the sacculi. Every branch of the nervus vestibuli that is distributed to an ampulla, dips, in

the greater number of animals, divided in the form of two flat fasciculi, and associated with ganglion cells (Leydig, Hasse), into the groove visible on the external surface, and runs in an almost straight direction through the tunica propria, as far as the epithelium of the crista acustica. This becomes two or

Fig. 311.

Fig. 311. Transverse section of the ampulla of Rana esculenta. 1, Roof of the ampulla; 2, semicircular canal; 3, epithelium lining the roof of the ampulla; 4, thick portion of the wall of the ampulla; 5, nerves, with cells scattered through them; 6 and 7, epithelium, with the auditory hairs; 8, fasciculi of nerves; 9, pigment.

three times thicker than elsewhere, and is bounded internally by a structureless basement membrane. This is not, however, the only supporter of the nerves, since the lower portion of the more or less rectangularly rising lateral walls of the ampulla,

which Steifensand has named the "plana semilunaria," also contains fine nerve fibres beneath the epithelium (fig. 310). As the primitive nerve fibres traverse the tunica propria, they approximate each other, becoming very fine in the neighbourhood of the crista, and losing their double contour. It is not difficult to demonstrate in the ampulla of Fishes that have been treated with perosmic acid, that a slender pale fibre, constituting the direct prolongation of a primitive fibre, as was first stated by Reich and Max Schultze, passes beyond the basement membrane of the ampullary crest without the intervention of any ganglion cell, and then divides into a great number of finer fibrils. Appearances of a precisely similar nature are so constantly found in specimens, both when recent and after maceration, that it is impossible to regard them as the results of manipulation. Hartmann has endeavoured to show that in Fishes the nerve fibres form loops in the crista acustica, though Henle had already disproved this view, which indeed may easily be shown to be erroneous from the examination of fine sections that have been subjected to imbibition. Hartmann's conclusion that the nerve medulla is mechanically forced through the basement membrane, giving the appearance of a divided axis-cylinder, cannot be correct if (1) pressure be avoided, and (2) *if openings in the basement membrane* which confer upon the nerve medulla its peculiar form, can be demonstrated to be pre-existent. On this point Max Schultze, F. E. Schulze, Odenius, Kölliker, Deiters, Hensen, Henle, and Hasse, all agree in stating that the pale fibres enter the epithelial layer as prolongations of the doubly contoured nerve fibres in the epithelium.* According to Max Schultze and Odenius, the pale axis-cylinder alone, but according to Hasse and v. Grimm, their delicate sheaths also, enter the epithelium. If, after treatment with perosmic acid, a comparison be

* Although Henle considers that the statements of Hartmann are directly negatived, he himself thinks the nerve fibres terminate by pointed extremities at the basement membrane (p. 777). Henle does not, however, hold himself justified in altogether denying the positive statements of others in regard to the entrance of the nerve fibres into the epithelium.

made in Fishes between the easily isolable axis-cylinder of the ampullary nerves and that of the fibres entering the epithelium, no histological difference is perceptible. With the use of high powers, I believe I have observed the simple division of the pale fibres in Frogs and Fishes even before the passage through the basement membrane. Further subdivision, however, always takes place after they have traversed it.

The layer of nerve-epithelium on the roof of the ampullary wall, that sometimes appears smooth, as in Man, Mammals, and Birds, sometimes folded, as in Fishes, varies in thickness in different animals from 0·016 of a millimeter (Bird) to 0·080 of a millimeter (Cyprinoid Fishes). In Mammals and in Man its thickness is intermediate to that of Birds and Fishes. The deepest layer of the nerve-epithelium resting on the basement membrane is soft, loose, and nucleated. It is thickest at the centre, and is bounded towards the free border by a well-marked line of demarcation, which resembles the membrana limitans externa of the human eye, and upon these the stiff hairs are seated. In the cyprinoids, Lang has described a peculiar cell layer which I have occasionally seen with great distinctness. These cells line the inner side of the epithelial layer; and to these the auditory hairs are attached. I regard the cavities in the epithelium, described and depicted by Lang, as accidental formations. The nerve-epithelium in the planum semilunare of the Fish becomes gradually wider from below upwards; then again narrower, and runs out, as seen in transverse sections, into a pointed extremity, to which the pavement cells of the upper portion of the ampulla are applied. Furthermore, at the point of transition of the crista acustica into the planum semilunare there is a less elevated epithelial layer. (See fig. 310.) The crista cruciata of the ampulla of the Bird, which projects to a considerable extent into the interior of the cavity, is covered throughout its whole extent by a rather thin layer of nerve-epithelium.

In the sacculi the nerve-epithelium is usually somewhat lower than in the ampullæ. Its transition into the adjoining columnar epithelium is here also more gradual; whilst in the sacculus rotundus, even at those parts which receive no nerves, the epithelium never presents so flattened a form as in the

membranous canals; that is to say, it never appears as a tesselated, but always as a transitional form of epithelium.

If the epithelial layer be broken up, the presence of several cell-forms may be demonstrated in it, in Man, Mammals, and

Fig. 312.

Fig. 312. Horizontal transverse section through the vestibule and sacculus rotundus of the human fœtus. 1, Cartilage; 2, nerves in the median wall of the vestibule; 3, crista vestibuli; 4, nerve epithelium in the sacculus rotundus; 5, auditory hairs; 6, transition of the nerve epithelium into 7, the flatter columnar epithelium; 8, the lateral wall of the sacculus rotundus; 9, utriculus, with the nerve epithelium; 10, tesselated epithelium of the utriculus.

Fishes. In the first place, there are *elongated columnar cells* of tolerably equal thickness, with a large nucleus at the central extremity. One end of these cells is broad, the other runs out

into a blunt cone. In Fishes and Frogs they contain a yellow pigment. These columnar cells, which were first accurately described by Leydig in the Eel, by Reich in Petromyzon marinus, and by Max Schultze in Sharks and Rays, form everywhere the inner boundary of the epithelium where there is no special cell-layer. In the Cyprinoids, low clear columnar cells of equal thickness, and a strongly refractile nucleus, are arranged close to one another upon the inner surface, and produce the appearance of a clear pale border at the centric extremity of the auditory hairs. No processes can be recognised in them; and were they not studied *in situ*, a single observation might lead to their being mistaken for simple cylinder cells from the marginal region of the planum semilunare. The epithelial forms present in the nerve-epithelium, and which are truncated at both extremities, appear to be only those *supporting* cells, between which the ends of the fibre cells penetrate.

These *fusiform*, thread, or rod-shaped cells (Spindel-Faden-oder Stäbchen-zellen) are present in much larger numbers than the columnar cells. They are the flask or thread cells which were originally described in similar terms by Max Schultze, and subsequently by Odenius, Kölliker, Henle, and Hasse. They are fusiform, with a long process running centrally and a rod-like process towards the periphery. The *pale* aspect they possess when fresh distinguishes them from other cells, and their behaviour with perosmic acid appears to deserve special notice. For if transverse sections of the ampullæ in Cyprinoids be examined under the microscope after the addition of osmic acid, it is soon observable that in proportion as the nerves become dark coloured, the epithelial border, with the auditory hairs also, though somewhat more slowly, assumes a brown tint.

Lastly, close to the inner boundary of the epithelial layer dark striæ occur, which may be followed to the surface. These dark but unequally thick striæ are situated at quite definite distances from one another. If the epithelial border be macerated for a somewhat longer time in the acid, the several cells can be isolated, and a *black stria* becomes apparent in the fusiform fibre cells, which I believe may really be considered to be enclosed within the cells. This appears to be the prolongation of the long fibre-like extremity of the cells, and is in direct con-

nection with the nucleus; that is, the cell nucleus is as dark-coloured as the fibre itself. The almost immeasurably fine fibre is prolonged peripherically, and in cells that still retain some remains of the auditory hairs the impression is given that no interruption occurs between the dark striæ in the interior of the fusiform cells and the auditory hairs. I have very fre-

Fig. 313.

Fig. 313. Diagram of the mode of termination of the auditory nerve. 1, Cartilage of the wall of the ampulla; 2, structureless basement membrane; 3, doubly contoured nerve fibre; 4, axis-cylinder traversing the basement membrane; 5, plexiform union of fine nerve fibres with interspersed nuclei; 6, fusiform cells with nucleus and dark fibre in their interior; 7, supporting cells; 8, auditory hairs.

quently observed these appearances in the ampullæ of the Cyprinoids; and the reaction occurring in these fusiform cells on the application of the above-named acid admits only of the interpretation that they are nervous structures. These observations are in accordance with the statements very recently made by

v. Grimm,* who has also observed the black coloration of the fusiform cells of the ampullæ of Cats, on the application of perosmic acid. A dark tinting of the nucleus is sometimes observable in the simple columnar cells, but I have never been able to see the dark striæ in these.

I am still doubtful in regard to the presence of the basal cells resting on the structureless border of the tunica propria described by Max Schultze, as I have been unable to bring them into view *in situ* in very thin sections. In one instance only in a large Salmon I thought I perceived striæ indicating a series of cells resting on the basement membrane. If the whole epithelial layer be detached from the tunica propria, no regular series of cells can be perceived resting upon the basement membrane, nor can several regular series of cells be distinguished in the detached layer of nerve-epithelium. M. Schultze has already made the observation that the basal cells do not occur through the whole extent of the ridge of the crista acustica, but are for the most part situated in the marginal regions.

As soon as the fine nerve fibres which it is impossible to distinguish from the isolated axis-cylinders have penetrated into the loose epithelial layer, they form *frequent anastomoses,* and thus produce a plexus which both at the points of intersection, as well as in the course of the fine fibrils, exhibits numerous enlargements. I have occasionally been able to bring this network very clearly into view. The nature of the swellings, however, still remains doubtful; for I am unable to regard them as ganglion cells, as Reich has done, notwithstanding that many recent observations tend to prove that nucleated enlargements in fine nerve fibres are to be considered as ganglionic elements, as in the case of the granule layers of the retina. Fibres proceed from the fine nervous plexus, which run vertically in the epithelium; and, from the results of numerous observations, I believe it may be admitted that the fibres which enter into the fusiform cells represent the continuation of the nerves. And if, on account of their assuming a black tint in perosmic acid, the dark striæ and the nucleus of the fusiform cells are to be regarded as nervous structures, we may

* *Bulletin de l'Academie impérial des Sciences de St. Petersbourg.*

also consider the auditory hairs as gradually attenuating processes of the flask-cells. These run up between the columnar epithelial cells by which the latter are supported, occupying the angular interspaces between their borders. It may further be remarked that though the auditory hairs do not become black in perosmic acid, yet they assume a brown tint earlier than any other tissue in the walls of the ampullæ.

The *nerve epithelium* of the ampullæ and sacculi thus presents a number of columnar supporting cells, between which are spaces and fine canals for the reception of the fusiform nerve cells, which last are to be regarded as bearing the terminal organs of the vestibular nerves. The observations of F. E. Schulze on a transparent fish (Gobius niger?) may here be mentioned, according to which the primitive nerve fibres are directly continuous with the auditory hairs. The stage of development of the animal from which his drawing was taken is such that the epithelial cells are probably not yet apparent.

According to Max Schultze and C. Hasse, stellate and partially pigmented cell forms occur in various classes of animals, situated between the simple columnar cells, in the neighbourhood of the nerve eminence of the crista acustica and of the macula acustica. The details of the special disposition of these cells is to be found in the beautiful treatises of those authors.

As regards the *auditory hairs*, the first observations upon the presence of ciliated epithelium in the membranous labyrinth were made by Ecker, Reich, and Leydig; but the true nature of the auditory hairs was first pointed out by Max Schultze. This observer described them as forming long stiff fibres which, gradually becoming more and more attenuated, are attached by their base to the nerve epithelium, and project into the fluid of the endolymph by their fine-pointed extremities, unless indeed, as I imagine, their extremity is covered by a peculiarly organised cap. That structure, which was observed and has been depicted by Leydig in the ampullæ of the Pigeon, I, with Max Schultze, regard as the detached epithelial investment of the crista acustica and its vicinity. In Fishes and Birds, however, I have observed a delicate structure composed of remarkably fine cells in that tract of the ampulla on which the auditory

hairs are seated, but into its precise relations I have gained no satisfactory insight.

The length of the auditory hairs amounts, according to Max Schultze, in the Ray tribe to 0·04 Prussian lines. They are disposed at definite distances from each other, and undergo

Fig. 314.

Fig. 314. Longitudinal section of the ampulla of a Bird. 1, Osseous wall; 2, periosteum; 3, space between the osseous and membranous canal; 4, roof of the ampulla adjoining the bone; 5, thickening of the crista acustica; 6, nerve fibres contained in it; 7, columnar cells of the floor in the vicinity of the nerve eminence; 8, line of demarcation between columnar and pavement cells; 9, pavement epithelium; 10, transition of the ampulla into the membranous canal.

very rapid changes in their form and appearance on the addition of various reagents. I have found the basal portion of the hair, both in Mammals as well as in Fishes and Frogs, even with the most careful manipulation, somewhat thicker than Schultze has described and pictured.

A difference in the course of the nerves in the very slightly thickened tunica propria of the macula acustica of the sacculus, as Henle has already pointed out, exists in the circumstance that

Fig. 315.

Fig. 315. Transverse section of the ampulla of Cyprinus carpio. 1, Roof of the ampulla; 2, lateral wall of the ampulla; 3, thickening of the lateral wall corresponding to the planum semilunare; 4, 5, 6, thickened floor of the ampulla, with the nerves; 7, nerve epithelium; 8, columnar cells; 9, planum semilunare; 10, the structureless bodies seated upon the epithelium; 11, pavement epithelium; 12, cupula terminalis.

they do not pursue the same linear course as in the ampullary crest; in other respects similar histological relations may be observed between the nerve and epithelium as in the ampullæ.

The vesicular structureless bodies which occur both upon the auditory hairs of the crista acustica, as well as closely compressed upon the epithelium of the planum senilunare, are particularly striking objects. I have observed them best in specimens of Cyprinus that have been macerated in perosmic acid. They here form an uneven layer covering the whole extent of the inner surface of the epithelium. (See fig. 315.) In these Fishes the auditory hairs appear sometimes to be held together by a glutinous material, a regularly shaped conical process (cupula terminalis) being observable on the epithelial surface of the ampullary crest (fig. 315), which in some of my preparations occupies more than two-thirds of the ampullary cavity. This is faintly striated, the striæ converging from the base towards the apex. The striæ, however, do not appear to be present in all parts of the eminence; for if the centre be brought into focus, a finely granular substance comes into view. Occasionally I have thought I have observed a cap upon its apex, composed of delicate cells. Lang has denied the existence of auditory hairs in the Cyprinoids, and in place of them has described the eminence itself as the terminal apparatus of the ampullary crest. I believe I can recognise in this the adherent auditory hairs. This subject is certainly worthy of further investigation.

Finally, two parts connected with the sacculus require to be mentioned, namely :—

(1) *The aquæductus vestibuli.*

(2) *The canalis reuniens.*

Böttcher has recently directed attention to the former. The process which extends from the posterior surface of the pars petrosa towards the vestibule, and lies in the so-called aquæductus vestibuli, has already long been known, and has been described at a remote period as the *aqueduct* of the vestibule. Böttcher has recognised the existence in this process of an epithelial canal, which is surrounded by nucleated connective tissue, and is lined on its uneven internal surface by vascular (?) tesselated epithelium exhibiting great similarity to the stria vascularis of the cochlear canal. The simple canal lying in the aquæductus terminates at the posterior surface of the pars

petrosa by a cæcal dilatation, and divides near the sacculus into two hollow ducts, of which one is continuous with the sacculus rotundus, whilst the other joins the utriculus; by this means the cavities of the two sacculi appear to be connected. On making a transverse section of the aquæductus vestibuli I have observed a moderately large convolute of vessels on one portion of its wall, and must therefore support the statement of Hyrtl, that it is destined for the reception of veins.

The canalis reuniens is limited to the sacculus rotundus. It was discovered by Hensen, and its existence corroborated by Reichert, Henle, and myself; it is attached to the periosteum, and is distinguished histologically from the wall of the sacculus only by the greater delicacy of its structure. This little canal brings the sacculus rotundus into connection with the ductus cochlearis, so that this forms the blind vestibular end of the most important cochlear segment of the labyrinth, just as the utriculus forms the blind vestibular end of the membranous labyrinth.

5. Otoliths.

The otoliths contained in the albuminous endolymph of the membranous labyrinth present many variations in different animals, in regard to their consistence, size, and form. They adhere tolerably firmly together by means of a clear tenacious substance. In Reptiles and osseous Fishes the delicately formed otoliths attain a considerable size, whilst in Birds, Mammals, and Man they either appear to be amorphous or are crystallized in the form of small rhombs, hexahedra, or octahedra. Otoliths of various size and form may however be found in the same animal.

Three or four otoliths of exceedingly pretty form occur in the osseous Fishes, where they are found both in the sacculi and in the ampullæ. In Man and Mammals they form the white spots of the maculæ acusticæ, and both here and in other animals they are maintained in position by a tenacious gelatinous substance, which Lang has described in the Cyprinoids as a peculiar fenestrated membrane (but which is regarded by Kölliker as a cuticular formation).

Deiters and Hasse admit the presence of a fenestrated cuti-

cular formation on the inner surface of the columnar epithelial cells in the otolithic sac of the Frog, by means of which its contact with the otoliths is prevented. I have observed this means of fixation of the otoliths very beautifully in transverse sections through the auditory organ of the Frog. Otoliths are essentially composed of carbonate of lime; according to Henle, however, after treatment with acids, there is a residue which is composed of organic substances (otolith cartilage). Leydig

Fig. 316

Fig. 316. Otoliths of different classes of animals. 1, From the Goat; 2, from the Herring; 3, from the Angler Fish; 4, from the Mackerel; 5, from Pterois volitans (after Breschet); 6, from the Pike; 7, from Cyprinus carpio; 8, from the Ray (after Leydig); 9, from Scymnus lichia (after Leydig); 10, from the Grouse (after Leydig).

has observed in the otolith of the Grouse, that, after treatment with bichromate of potash, peculiar lines occur at the two poles, which converge towards the centre (fig. 316, 10). It still remains to be mentioned that in Man and Birds, even when the vestibule is quite uninjured, otoliths may be observed in considerable numbers in the membranous semicircular canals, especially in the horizontal one, and according to Hyrtl in the fluid of the cochlea. In these cases it is impossible to admit

that they have escaped into the semicircular canals from the utriculus.

6. The Fenestra Ovalis, and its connection with the Base of the Stapes.

The majority of authors describe the insertion of the base of the stapes into the fenestra ovalis as being of a very simple nature, whilst I, on the contrary, find that it is rather complicated. That Soemmering* had already noticed this, is evident from his remark, "that the basis of the stapes is attached to the fenestra ovalis by a delicate articular capsule." But it is impossible to determine from this brief expression whether Soemmering meant to indicate by the term articular capsule the existence of a proper joint, or only the presence of a fibrous layer resembling a fibrous articular capsule. Several writers speak of a simple fibrous union, to which they apply the term Ligamentum orbiculare baseos stapedis. It was reserved for the active Englishman, Toynbee, to furnish an exact description of the mode of connection of the base of the stapes with the fenestra ovalis.

The difference in form between the *anterior and the posterior border of the base of the stapes*, which in a physiological point of view is certainly of importance, was first noticed by Toynbee,† by whom also the hyaline cartilage between the fenestra ovalis and the base of the stapes was first described.

If in a successful horizontal section the anterior extremity of the base of the stapes be compared with the posterior, it is observable that besides the thickening which exists at these spots, the moderately broad posterior surface of contact forms almost a right angle with the vestibular surface of the base of the stapes, and that the base towards the posterior limb of the stapes runs off into a kind of process (fig. 317). The surface of contact at the anterior margin of the base is somewhat narrower than at the posterior, and forms an acute angle with its vestibular surface, so that the whole anterior extremity which projects beyond the corresponding limb appears somewhat longer than the

* *Vom Bau des menschlichen Körpers.* Frankfort, 1796. Theil ii., p. 12.

† *British and Foreign Medico-Chirurgical Review*, 1853.

posterior; and it is very conceivable that, owing to the obliquity of the surfaces, and the greater length of the anterior margin of the base of the stapes, a certain amount of resistance is opposed to the action of the voluntary musculus stapedius.

The above-mentioned moderately thick borders of the base of the stapes are invested by a *lamella of hyaline cartilage,*

Fig. 317.

Fig. 317. Horizontal transverse section through the base of the stapes at its insertion into the posterior border of the fenestra ovalis. 1, Bony margin of the base, with its investment of hyaline cartilage; 3, thin osseous lamella of the basis; 4, angle between the crus of the stapes and the projecting border of the base; 5, posterior border of the fenestra ovalis, with its investment of hyaline cartilage; 6, cartilage on the vestibular surface of the base, with its perichondrium; 7, ligamentum baseos stapedis vestibulare; 8, Ligamentum baseos stapedis tympanicum; 9, layer of elastic fibres; 10, spaces between the fibres; 11, osseous trabeculæ; 12 and 13, musculus fixator baseos stapedis.

which varies in thickness from 0·012—0·024 of a millimeter. The hyaline cartilage dips into the inequalities of the bone, in order that here, as in other osseous junctions of the body, the opposite surfaces may be uniformly applied to each other. It is not, however, the anterior and posterior borders of the base of the stapes that are alone invested with cartilage, but a layer of this substance covers the whole vestibular surface of the stapes.

The cartilage at the last-named part is invested by nucleated fibrous tissue, constituting the perichondrium, which is continuous with the lining membrane of the vestibule. The homogeneous matrix of the cartilage is distinguished from the adjoining osseous tissue by its yellowish tint, and in tinted specimens the rounded cartilage cells are brought clearly into view in consequence of the intense colour of their nuclei, as compared with the colourless matrix.

The cartilage cells undergo a change in form near the centre of the vestibular surface of the base of the stapes, becoming elongated, with their longest diameter running from before backwards.

The margin of the fenestra ovalis also possesses a cartilaginous investment. The thickness of this at the posterior border is equal to that covering the opposite surface of the base of the stapes: anteriorly it measures from 0·040 to 0·048 of a millimeter. The cartilage terminates more abruptly towards the tympanic cavity than in the vestibule, where it reaches beyond the margin of the fenestra ovalis, and becoming thinner extends for some distance upon the surface of the vestibule.

A layer essentially composed of *elastic tissue*, and equal in thickness to the hyaline cartilage, is continuous with this both at the fenestra ovalis and at the border of the base of the stapes; the layer is of very close texture, and it becomes very conspicuous in macerated specimens, in consequence of strongly imbibing the colouring material. The fibres run from one cartilage towards the other, and at the point where the opposite sets meet *a system of lacunæ is formed by their plexiform inter communication*, which is filled with fluid. Towards both the *vestibule* and the *tympanic cavity* this dense elastic tissue extends from the one cartilage to the other, forming a *ligamentum orbiculare baseos stapedis vestibulare*, and in the tympanic cavity a weaker *ligamentum orbiculare baseos stapedis tympanicum*. The latter is continuous with the mucous membrane of the tympanic cavity, without however being so sharply defined at its circumference, as is shown in fig. 318.

At the upper and lower borders of the base of the stapes the nature of the connection changes in consequence of the uniformly thick circumference of the base being bevelled off

towards the tympanic cavity, so that the surfaces of contact are somewhat smaller than at the already described anterior and posterior extremities. A cartilaginous investment is, however, here also present, which augments in thickness to some extent towards the middle of the vestibular surface of the basis. The connection with the cartilaginous investment of the margin of the fenestra ovalis is established by means of a layer of

Fig. 318.

Fig. 318. Horizontal section through the anterior margin of the base of the stapes at its attachment to the fenestra ovalis. 1, acute angle made by the margin of the basis with the cartilage; 2, base of the stapes; 3, anterior crus; 4, margin of the fenestra ovalis invested by hyaline cartilage; 5, ligamentum baseos stapedis tympanicum; 6, ligamentum baseos stapedis vestibulare; 7, elastic fibrous layer of the fenestra ovalis; 8, the same at the base of the stapes; 9, lacunar system in the centre of the fibrous layer. The two ligaments at the base of the stapes are not so sharply defined in the preparations themselves as in the figure.

elastic fibres, in the middle of which intercommunicating spaces occur, though more sparingly than in that of the anterior and posterior margin.

The articulation of the stapes with the fenestra ovalis is consequently neither a pure syndesmosis nor a synchondrosis, but constitutes a mode of connection that, if rightly placed in the category of the other joints, would be included in the amphiarthroses, from which it differs only in the circumstance

that there are a large number of intercommunicating cavities, whilst in the amphiarthroses generally there is only a single irregularly shaped cavity.

If we altogether disregard mere nomenclature, it appears from our description that the base of the stapes is attached to, or inserted into, the fenestra ovalis in quite a peculiar manner, a fact which indeed Helmholtz has established experimentally. This observer has demonstrated that the mobility of the base of the stapes is very small, the greatest excursion it can make not exceeding 1-18th to 1-24th of a millimeter. According to the earlier accounts of the mode of attachment of the base of the stapes with the fenestra ovalis, a considerable degree of mobility occurs between them. All the diameters of the osseous fenestra ovalis are, however, so far diminished by the elastic cushion of the hyaline cartilage that the base of the stapes, which is also covered with cartilage, is received into it, and but little room for movement consequently remains. I have still to call attention to a structure on the tympanic surface of the base of the stapes, which, from the observations I have hitherto made, I must regard as a muscle of vegetative life—the *musculus fixator baseos stapedis*.

At about the distance of a millimeter from the fenestra ovalis, a narrow crest of bone, with a transverse diameter of about 0·080 of a millimeter, springs from the posterior and inferior border of the base of the stapes, and projects into the tympanic cavity. In surface views this appears in the form of a low sinuous elevation which terminates with a blunt point that is opposite the projecting border of the base of the stapes. Its importance is only recognizable in transverse sections. The mucous membrane presents the same relation to this crest of bone as to the others that project into the tympanic cavity.

Forming a direct continuation of this ridge is a *yellowish* dense tissue, which is attached to the angle between the crus of the base of the stapes and the somewhat everted part of the base. This tissue is connected and continuous, however, not only with the bone, but also with the cartilaginous investment (fig. 317).

In macerated transverse sections which have been subjected to imbibition, long coloured striæ are visible, which, in isolated

specimens, appear in the form of fusiform cells, and which I at present regard as contractile fibre cells.

This fixator baseos stapedis is confined not only to the posterior extremity of the base of the stapes, where it is thickest, but it is continued towards the upper border, and the direction of its action is consequently antagonistic to the voluntary musculus stapedius; for it fixes the basis at that part which is pressed towards the vestibule by the unilateral action of the musculus stapedius.

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IV.

THE AUDITORY NERVE AND COCHLEA.

By W. WALDEYER.

General View of their Comparative Anatomy and Development.

Whilst the auditory apparatus treated of in the preceding chapter—the semicircular canals and utriculus—already attain their complete development in the majority of Fishes, the second division of the membranous auditory labyrinth—the *cochlear apparatus*—is essentially developed as a constituent of the organ of hearing in the higher classes of animals. The cochlear apparatus includes the *sacculus*, the histological characters of which are analogous to those of the utriculus (see the preceding chapter), and a cæcal prolongation of the sacculus—the *ductus cochlearis*.

The first trace of a *ductus cochlearis* is exhibited by the osseous Fishes, in which, according to the excellent description of Hasse (25), a small projection of the sacculus (fig. 319, 1 *C*), called by Breschet (5) the *cysticula*, is to be regarded as the rudiment of the cochlea.

Amongst Amphibia, several portions of the sacculus can be distinguished as belonging to the cochlea, though, with the exception of a small and more independent projection which corresponds to the cysticula of the Fish and the lagena of the Bird, they scarcely rise above the level of the wall of the sacculus (otolith sac), and rather resemble thickenings of the saccular walls provided with peculiar nerve ends (Deiters, 15; Hasse, 24).

The cochlear apparatus of Reptiles and Birds is still further developed. In Reptiles, the several divisions of the

cochlea appear in the form of a cone projecting beyond the plane of the sacculus, especially well marked in the Crocodile, which most nearly approximates Birds. In the latter, as Hasse (68) has shown to be probable, the sacculus and utriculus are fused into an alveus communis (fig. 319 II., *US*.

Fig. 319.

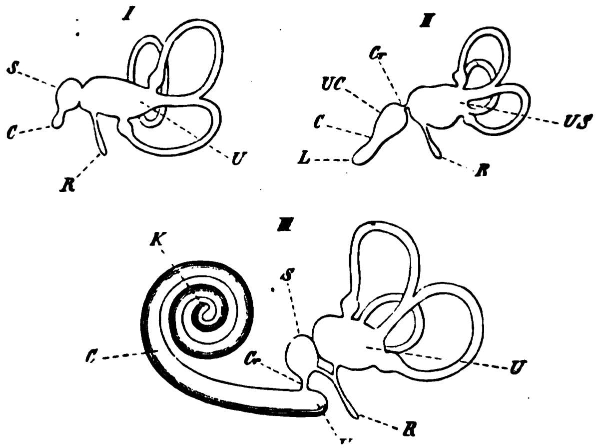

Fig. 319. Three diagrams to show the relations of the auditory labyrinth in the Vertebrate series.

I. Type of the labyrinth in the Fish. *U*, Utriculus with the semicircular canals ; *S*, sacculus ; *C*, cysticula ; *R*, aquæductus vestibuli.

II. Type of the labyrinth in the Bird. *US*, alveus communis ; *C*, cochlea ; *UC*, commencement of the cochlea ; *L*, lagena ; *Cr*, canalis reuniens ; *R*, aquæductus vestibuli.

III. Type of the labyrinth in the Mammal. *U*, *S*, *Cr*, as before ; *R*, aquæductus vestibuli, dividing into two crura for the utriculus and the sacculus ; *C*, ductus cochlearis, with *V*, the cæcal pouch of the vestibule, and *K*, the cæcal sac of the cupola.

The cochlear passage (*C*) is considerably elongated, and several divisions or segments may be distinguished in it, as the commencement or cochlea proper (*UC*) and the flask-shaped terminal segment or lagena (*L*) of Windischmann. Here is seen also the first indication of a spiral course in the cochlear canal. The communication of the latter with the alveus is effected by a narrow passage, the canalis reuniens of Hensen, which, cording to the observations of Hasse, appears frequently to

undergo obliteration in adult Birds. I have myself frequently found only a narrow tube at this point.

Fig. 319 III. represents the type of the labyrinth in Mammals; here the semicircular canals and the cochlear portion communicate with one another only through the intermediation of the *aquæductus vestibuli* (*R*) (Böttcher, 3). See the preceding chapter. The ductus cochlearis (*C*) has undergone extraordinary development, and forms the principal part of the labyrinth; as is already seen in Birds, it has become entirely distinct from the sacculus, and is only in connection with it by the narrow canalis reuniens (*Cr*). The canalis reuniens proceeds from the wall of the ductus—the membrana Reissneri (see below); it opens into the cochlear passage almost at a right angle, so that a small cæcal sac exists beyond its point of attachment—the vestibular cæcal sac (*V*) (Reichert). The other end of the duct likewise terminates blindly, forming the *cæcal sac of the cupola* (*K*) (Reichert). The canalis reuniens and the two cæcal sacs are lined by a short columnar epithelium, and receive no fibres from the auditory nerve. The cochlear canal, which here properly answers to its name, is wound spirally around a bony axis, the *modiolus*. The number of turns varies in different animals from one and a half to five. They sometimes lie nearly in one plane, like the shell of the Planorbis (Cetacea); sometimes, on the other hand, they may coil steeply around the modiolus, as in Clausilia (Guinea-pigs); we may thus have flat and steep coiled cochleæ.

Whilst I refer to the preceding chapter for an account of the sacculus, I consider it to be advantageous in regard to the somewhat complicated structure of the cochlea to precede its histological description by a short account of the bony capsule and of the position of the ductus cochlearis, together with a sketch of its development. I shall commence with the cochlea of Mammals and of Man.

A median section carried through the axis of the human cochlea, as in fig. 320, exhibits a tubular canal imbedded in the hard mass of the temporal bone, which, constantly becoming narrower, runs spirally to the apex of an also gradually attenuating axis, and terminates by a blind extremity in the so-called cupola. This canal is traversed throughout its whole length by

a partly osseous and partly cartilaginous septum, the *lamina spiralis*, which divides externally into two laminæ that pass to the osseous walls of the cochlea, and enclose the ductus cochlearis between them (fig. 320, *L Sp*). In this way the osseous canal of the cochlea is divided by the ductus cochlearis and its two attachments—the osseous at the modiolus, and the membranous towards the outer wall—into two chambers, the *scala tympani* (*ST*), and the *Scala vestibuli* (*SV*), which only communicate with one another at the cupola of the cochlea by a fine aperture, the *helicotrema* of Breschet. The scala tympani terminates cæcally, being cut off by the membrane of the fenestra rotunda from the tympanic cavity; the scala vestibuli communicates directly with the perilymphatic space of the vestibular sacculus. The situation of the ductus cochlearis in the cochlear mass corresponds therefore to the semicircular canals and sacculi in the other part of the labyrinth (see the preceding chapter). Like these, it is attached excentrically to the external wall of the canal, and indeed by its opposite sides.

The median lamina of attachment, (with reference to the axis,) which at the same time supports the nerves, is here very much elongated and ossified (lamina spiralis ossea); the lateral lamina of adhesion, which especially supports the vessels (fig. 320, the connective tissue between *h* and *b*; figs. 321 and 322, *e e*), forms a thick cushion of connective tissue, which is semilunar on section (*ligamentum spirale*, Kölliker). See below.

The ductus cochlearis (fig. 320, e—e_4; figs. 321 and 322, *D C*) forms in adults a tubular cavity, which is triangular in section, and is enclosed by a connective-tissue membrana propria; towards the tympanum it is bounded by the *membrana basilaris* (*f L sp*), which is continuous with the *crista spiralis* (*R*—*Cr*, figs. 321 and 322), in the *sulcus spiralis internus* (*S. sp. i*), (the entire tympanal wall is included between the letters *R* and *L sp*,) towards the vestibule, by the *membrane of Reissner* (*f f*, fig. 320; R R_{I}, fig. 321); laterally it is bounded by a vascular layer of connective tissue, which is continuous with the periosteum of the cochlea by means of the above-mentioned semilunar cushion of connective tissue (*e e*, figs. 321 and 322). Towards the inner side the membrana Reissneri and crista spiralis join at a more or less acute angle.

Fig. 320.

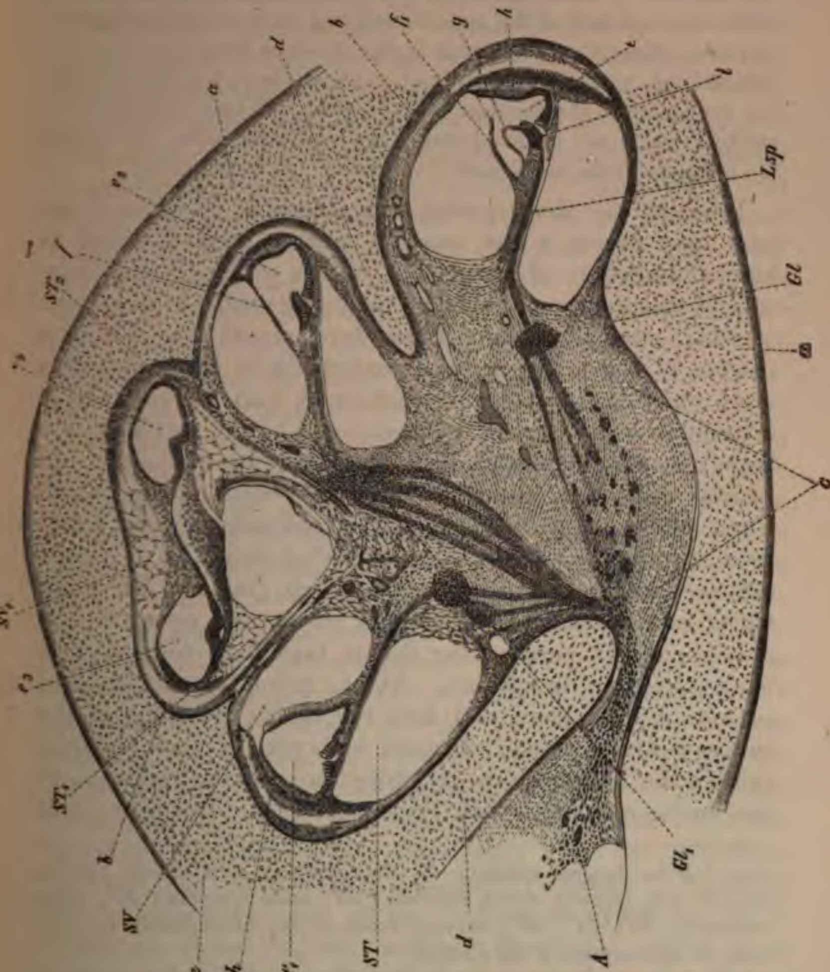

Fig 320. Section of the cochlea in a human embryo of four months, magnified thirty diameters. *a a a*, Cartilaginous capsule of the cochlea; *bb*, perichondrium; *c*, mucous-tissue matrix of the modiolus; *dd*, cartilaginous septa of the several turns of the cochlea; e—e_4, sections of the ductus cochlearis; $f f_1$, membrane of Reissner; *g*, membrana tectoria, slightly separated from the subjacent tissue; *h*, rudiment of stria vascularis; *i*, rudiment of the later appearing organ of

In the subsequent pages we shall call the surface looking towards the modiolus of the cochlea the "internal" (mesial), and that turned to the external wall of the osseous cochlear canal as the "external" (lateral). Everything that runs in the direction from the axis to the external wall, we name "radial," and, on the contrary, everything following the course of the cochlear walls, "spiral" (Henle). Lastly, those surfaces which are turned towards the vestibular scala, or towards the tympanal scala, are termed "vestibular" or "tympanic." *

Touching the development of the cochlea, to which I can here only devote a few remarks, it may be stated, that in human embryoes of from eight to ten weeks of age, three several textural constituents are distinctly visible in the region of what subsequently undergoes development into the pars petrosa of the temporal bone; externally is a cartilaginous mass, which is at this period continuous with the rest of the cartilaginous basis cranii; next, enclosed by the cartilage, is a large spheroidal mass of embryonal mucous tissue, within which, again, the epithelial labyrinth-vesicle is imbedded. From the same part of the latter that subsequently corresponds to the sacculus, a hollow epithelial projection is thrust out, even before the eighth week, which, gradually becoming wider, penetrates into the mucous tissue, and, owing to the presence of the surrounding denser capsule, is compelled to wind spirally in its soft bed. At one point the cartilaginous capsule is incomplete, and here the ramus cochlearis of the auditory nerve enters. Human embryoes of three months exhibit the hollow epithelial projection, and the rudiment of the ductus cochlearis, with its several coils. In embryoes of

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Corti; *L sp*, lamina spiralis; *Gl*, Gl_1, ganglion spirale with various afferent and efferent nerve fasciculi; *ST*, scala tympani; *SV*, scala vestibuli; ST_1, SV_1, ST_2, mucous tissue of the subsequently forming scalæ in the last turn of the cochlea.

* There is scarcely any region of the body so small in extent as that of the cochlea which possesses so rich and complicated a nomenclature. The confusion is not diminished by the practice, little worthy of commendation, but adopted by many authors who have given a fresh description of long-known structures, of inventing a series of new names. Perhaps the terms now employed may not appear to be inappropriate to my fellow-workers. Scarcely any new ones have been added, whilst many superfluous and duplicate terms have been simplified.

four months, the development of the scalæ commences, as well as of the parts contained in the duct (fig. 320).

The former originate in the retreat (Verflüssigung) of the mucous tissue, to the two sides of the ductus cochlearis (see fig. 320, where this tissue still remains in the last coil), whilst, in order to form a septum between the two coils, it undergoes ossification, the cartilaginous capsule however, participating to some extent in the process (fig. 320, *d*). Moreover a cord proceeding from the duct, and extending to the axis of mucous tissue, remains persistent, in which at a very early period the fibres and ganglion cells of the auditory nerve are visible (*L sp* and *Gl* in fig. 320). This cord partly ossifies near the axis, forming the lamina spiralis ossea, and always continues to be fused in a peculiar manner with the fibrous membrana propria of the canal, which is already capable of being demonstrated as a special layer. The membrana propria is developed in exactly the same manner out of the mucous tissue around the ingrowing epithelial tube, as is the theca of the Graafian follicle, or the fibrous wall of the utriculus and semicircular canals. We find here a recurrence of the same process as that stated by His (69) to occur in the development of epithelial masses in a matrix of connective tissue. The epithelial structures appear to exert a formative stimulus upon the fibrous investment, resulting in an abundant cell proliferation immediately around the epithelial tube, from which at a subsequent period the membranæ propriæ of the originally naked epithelial masses are developed. We learn these facts, especially in reference to the ductus cochlearis, from the illustrations of E. Rosenberg (49), the correctness of whose fig. 1, in plate ii., I can entirely confirm. Ultimately the mucous-tissue axis of the cochlea, in which the nerve fibres are imbedded, also ossifies. In all the ossified parts remains of the mucous tissue persist in the form of a delicate periosteum. A proper perichondrium is indeed visible at an early period on the inner wall of the cochlear capsule, and with this the remains of the mucous tissue of the scalæ subsequently coalesce.

The epithelium of the ductus cochlearis (fig. 320, e—e_4) is genetically identical with the epithelium of the labyrinth-

Fig. 321.

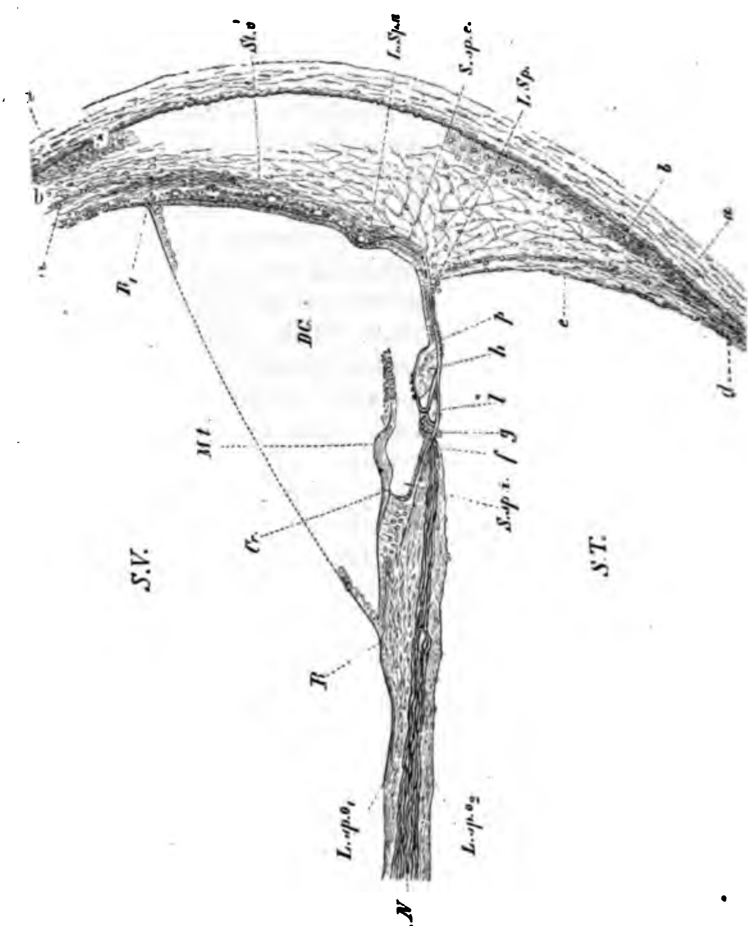

Fig. 321. Vertical section of the first turn of the cochlea, from a child of a year and a half old, magnified 100 diameters. The position of the membrana tectoria is given from other preparations of the same cochlea. *SV*, Scala vestibuli; *ST*, scala tympani; *DC*, ductus cochlearis; *L sp o*$_1$, vestibular, *L sp o*$_2$, tympanal lamella of the lamina spiralis ossea; *N*, cochlear nerve; *aa*, bony wall of the cochlea; *bb*, periosteum; *ee*, cushion of connective tissue (ligamentum spirale of Kölliker), partly detached from the bony wall, and condensed near the ductus cochlearis to form a special fibrous wall to this canal; *St v*, stria vascularis; *d*, point at which the periosteum and the connective-tissue

vesicles; and hence, if we are disposed to follow the statements of Remak, we must refer their origin to the horny lamina of the embryo, by the inversion of which into the matrix of the fibrous portion of the temporal bone these vesicles arise. The traces of this involution betray themselves, as Böttcher (3) has recently shown, in the epithelial investment of the aquæductus vestibuli, still present in adults (recessus labyrinthi of Reissner) which in the Plagiostomi actually opens by a fine pore on the surface of the skin. Stricker (64), Schenk (63), and Török (65), have demonstrated in the case of the Batrachia, that it is not so much the horny lamina as the immediately subjacent layer, termed by Stricker the "sensorial layer," the involution of which leads to the formation of the auditory labyrinth, a statement that has recently been corroborated by van Bambeke (58). In this case there would be complete harmony in the mode of development between the labyrinth and the retina, as well as the olfactory vesicle, all of which parts, together with the central nervous system, must be referred to the sensory layer. As Kölliker has pointed out, the organ of Corti, the most essential constituent of the cochlea, is developed from the involuted epithelium of the ductus cochlearis, and I shall recur to the most remarkable details of this process, so far as they are at present known, in the course of my description of that part.

In the above rude outline of the comparative anatomy and developmental history of the cochlea, we obtain the general ideas requisite for the right comprehension of its histology.

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cushion coalesce; *L Sp*, ligamentum spirale of Henle; *L Sp a*, ligamentum spirale accessorium, with the vas prominens; *S sp e*, sulcus spiralis externus; *R—R₁*, Reissner's membrane, the two ends being alone preserved; *R—Cr*, crista spiralis; *Cr*, its most prominent portion (auditory teeth) in transverse section; *Mt*, membrana tectoria; *S sp i*, sulcus spiralis internus; *f*, point where the nerves traverse the lamina spiralis (habenula perforata); *f—L Sp*, membrana basilaris; *f—p*, Corti's organ; *Cr—p*, zona denticulata; *g—h*, zona arcuata; *p—L Sp*, zona pectinata, with epithelium; *g*, region of the internal hair cells (internal portion or slope of the roof, innere Abdachung); *l*, thinnest part of the membrana basilaris beneath the arches of Corti; *h*, region of the external hair cells (external portion or slope of the roof, äussere Abdachung).

We learn at once to distinguish the original soft parts of the cochlea from their osseous capsule, formed by the petrous bone; and we learn to recognize the scalæ as secondary structures formed around the principal canal of the cochlea, the ductus cochlearis, the epithelial lining of which is destined ultimately to constitute the very nucleus of the whole apparatus. The arrangement, therefore, which commends itself as being most appropriate for an histological description of these parts is, in order: the osseous shell, with its periosteum; the structures termed the modiolus and the lamina spiralis; the scalæ, with the parietal layer of the ductus cochlearis, composed of connective tissue; and lastly, the epithelial investment of the latter. To this may be appended the consideration of the terminal expansion of the nervus acusticus, in which also all that is needful to be mentioned in respect to the histological relations of the trunk of the auditory nerve will be given.

Capsule of the Cochlea and Membrana Propria of the Ductus Cochlearis.

In regard to the osseous capsule of the cochlea, it may be sufficient to call attention to the compact structure of its inner layers, which are poor in bone cells, and form a kind of tabula vitrea. On the contrary, the portions of the cochlea which have ossified from mucous tissue, as the modiolus and lamina spiralis, are of a more spongy nature, and contain numerous medullary cavities, together with canals for bloodvessels and bones. One of these canals, the *canalis ganglionaris*, discovered by Rosenthal (Claudius, Vietor, 55), conceals the *ganglion spirale* of the auditory nerve, and usually winds round the modiolus at the base of the lamina spiralis (figs. 320 and 322).

In Man this canal is traversed by many trabeculæ of bone, so that strictly speaking it forms a tubular system of cavernous spaces, the cavities of which are occupied by the ganglion cells and nerve fibres.

An account has already been given of the periosteum of the cochlear wall, as far as regards its relations to the ductus cochlearis, and I may refer to the preceding chapter for a

description of the periosteum of the labyrinth. I may, however, just mention the very frequent occurrence of stellate pigment cells in it, closely resembling the stroma cells of the choroid. They are very numerous both in Man and in the Rat. The internal surface of the periosteum, with the exception of the tympanic surface of the membrana basilaris, where, like

Fig. 322.

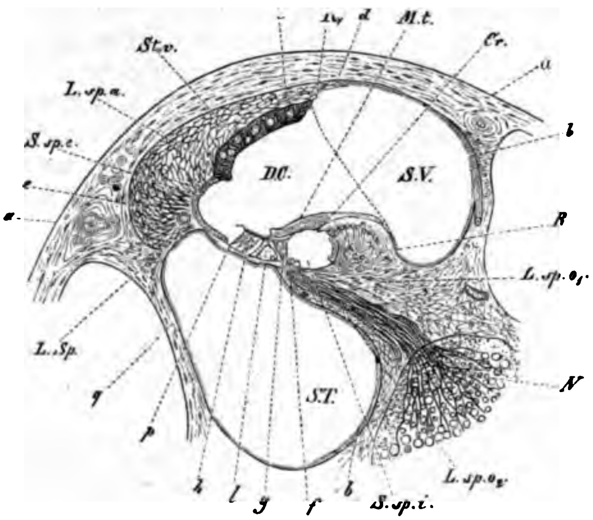

Fig. 322. Vertical section through the second turn of the cochlea in Vesperugo noctula (the membrana tectoria inserted in accordance with its position in another specimen), magnified 100 diameters. *N*, cochlear nerve, with a part of the ganglion spirale; *e e*, cushion of connective tissue more firmly connected with the periosteum than in fig. 221; *L Sp*, ligamentum spirale of homogeneous character, with a bloodvessel immediately external to it; *R* R_1, Reissner's membrane, indicated by a punctated line; *h*, external portion or slope of the roof (Abdachung), with the three external hair cells *in situ*. The internal hair cells, as well as the epithelium of the sulcus spiralis internus, not completely preserved. The rest of the lettering as in fig. 321.

Kölliker (30), I have been unable to discover them, is covered by a single layer of large flat nucleated cells, which, when subjected to the action of nitrate of silver, presents the same markings as are visible in lymph sacs or serous membranes. Luschka (70) has already referred to this point, and his state-

ments may also be compared with those of Reichert (44, 45). The researches of Schwalbe (71) have satisfactorily shown that the scalæ correspond to a lymphatic cavity, or still more closely to the perichorioideal space of the bulbus oculi, or to the arachnoideal space of the brain. (See also the statements of Kölliker, 62, 34.)

The membrane of the *fenestra rotunda* belongs both to the mucous membrane of the tympanic cavity, and to the periosteum of the cochlea; and, in accordance with this, presents two layers composed of finely fibrillar connective tissue. The tympanal layer is the thicker of the two, is traversed by numerous vessels, and is invested with the epithelium of the tympanic cavity ; the vestibular layer looking towards the corresponding scala is directly continuous with the periosteum of the first turn of the cochlea.

Brief allusion may be here made to the *aquæductus cochleæ*, which as is generally admitted (see especially the account given by Hensen, 27, and Henle, 26) conveys only a fibrous process of the dura mater, and a vessel running to the vena jugularis interna. The opening of the aquæductus is close to the commencement of the scala tympani.

In proceeding to the description of the principal portion of the cochlea, the *ductus cochlearis*, we may first take a bird's-eye view of its constituent parts as exhibited in such transverse sections as figs. 321 and 322.

In addition to what has already been stated on p. 134, in regard to the position, form, and boundaries of the ductus, I may state in the first place that the vestibular wall, or *membrane* of Reissner, is inserted externally to the semilunar cushion of connective tissue (*e e*). The point of attachment, *angulus vestibularis* (R_1), is marked by a slight projection (Henle). The external point of attachment of the tympanal wall (*R—L sp*) is formed by a strong process, triangular in section, termed the *ligamentum spirale* (*L sp*). Between the two processes is the outer wall of the duct, in which we may recognize the vascular *stria vascularis* (*St v*), as well as a third small elevation, the *ligamentum spirale accessorium* (*L sp a*), with a vessel, the *vas prominens* of Henle, forming the tympanual limit of the stria; and lastly, situated between this eleva-

tion and the membrana basilaris, the *sulcus spiralis externus* (*S sp e*). The two chief portions of the tympanal wall, already named, the *crista spiralis* and the *membrana basilaris*, are best separated from one another by the point of entrance of the cochlear nerves into the cavity of the ductus cochlearis. The

Fig. 323.

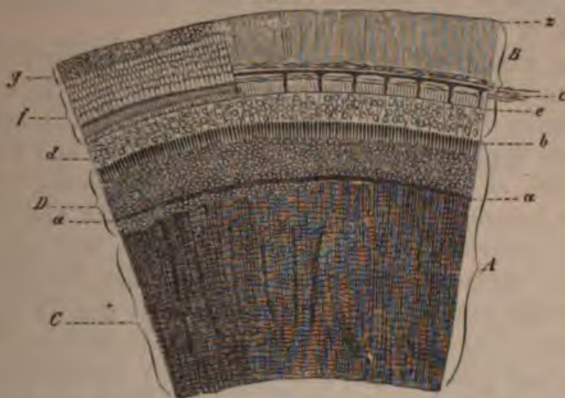

Fig. 323. Surface view of the lamina spiralis of Man in the second turn, as seen from the vestibule, and magnified 30 diameters. From a woman aged 28. The membrane of Reissner and the membrana tectoria have been removed. The zonular or girdle-like arrangement of the several parts is very apparent. *A*, lamina spiralis ossea; *B*, lamina spiralis membranacea; *C*, dark zone of the lamina spiralis ossea (covered only by a thin periosteal layer and the epithelium of the vestibular scala; *D*, crista spiralis, with a brighter appearance; *b*, its projecting border, with the rows of auditory teeth; *a*, line of attachment of the membrane of Reissner; *a—z*, the part of the lamina spiralis belonging to the ductus cochlearis (tympanal wall of the duct); *c*, vas spirale faintly seen through the tympanal surface, accompanied by spiral bands of connective tissue; *d*, floor of the sulcus spiralis internus, with fibres running radially on the tympanal surface glimmering through *e*, lines in which lie the holes of emergence of the nerve fibres; *f*, organ of Corti; *g*, external epithelium (*f* and *g* detached from the right half of the specimen).

crista spiralis (*R—f*) rests upon the most external portion of the lamina spiralis ossea, and is composed of two lips, the *labium vestibulare* (fig. 325, *c*) (Henle), which terminates in a sharp process (*Cr*), projecting into the ductus cochlearis and

the *labium tympanicum* (of Henle) (fig. 325, *a*), which lies in the same plane with the membrana basilaris, and with the labium vestibulare forms the boundary, the *sulcus spiralis internus* (*S sp i*). From the point of entrance of the nerve (fig. 323, *a*) to about the middle of its length, the organ of Corti is superimposed upon the basilar membrane; but from thence, as over the rest of the internal wall, there is only a simple short columnar or cubical epithelium.

If we examine the tympanal wall after removal of the membrane of Reissner, its several portions appear like so many spiral girdles or zones, as shown in fig. 323. To this structure the names applied by Todd and Bowman, Corti and Kölliker, refer: such as the zona denticulata and pectinata, together with the habenula denticulata, sulcata, perforata and arcuata, forming subdivisions of the zona denticulata, and respecting which the explanation of the lettering in figs. 321, 322, 323, and 324, may be consulted. These terms may now be regarded as obsolete. The size of the ductus cochlearis decreases, though not to a very great extent, according to my measurement (see the tables subjoined), as its three successive turns pass towards the cupola.

The membrane of Reissner is composed of a thin basal lamella of connective tissue, supporting vessels, and covered on the vestibular surface by a large-celled serous endothelium, and upon the tympanal surface by a single layer of cubic cells (figs. 321 and 324).

The relations of the *external wall* of the membranous duct of the cochlea are of a more complicated nature (figs. 321 and 322, *e e*). The already frequently mentioned cushion of connective tissue, which is semilunar in section, exhibits, especially in young individuals, three distinct layers: internally the *membrana propria* of the ductus cochlearis, with the stria vascularis; externally, the *periosteum;* and between the two a *loose connective tissue*, which, in embryoes, tears easily, and thus permits the ductus cochlearis to be detached from the cochlear capsule. The stria vascularis is a particularly vascular portion of the membrana propria. Between the numerous capillaries is a little adventitious connective tissue, whilst the epithelium, composed of small cubic cells, rests immediately

upon the vessels. Here and there the vessels project in the form of small loops. These last are particularly well marked in Birds, on the roof of the ductus cochlearis in the so-called *tegmentum vasculosum* (Deiters, 14), which corresponds to the stria vascularis of Mammals. The epithelium of the tegmentum in Birds also presents some peculiarities; for between the clear cubic cells—and I can fully corroborate the statement of Deiters on this point—are moderately large nucleated dark granular structures of nearly uniform size, the cell protoplasm of which appears quite like felt. A clear slender portion of irregular triangular or quadrilateral shape, to which small hairs are sometimes attached, projects from the free surface of the felt-like body of the cell. The opposite extremity runs out into a sharp point (fig. 336, *E*).

A very well-marked columnar epithelium occurs again in Mammals upon the *sulcus spiralis externus*. The layer immediately subjacent to this consists, in adults, of a homogeneous glass-clear tissue, which is directly continuous with the triangular process of the *ligamentum spirale*, and from thence passes into the homogeneous layer of the basilar membrane.*

A reference given by Schweigger-Seidel (72) shows that Böttcher (4) has again taken up the view of Todd and Bowman (54), long ago set aside by Kölliker (32), to the effect that the ligamentum spirale contains smooth muscular fibres. After much investigation, however, I must coincide with the negative view of the question taken by Kölliker.

The *crista spiralis* has presented no slight difficulties to the investigators of the cochlea—difficulties in my opinion occa-

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* It does not appear to be agreed upon as to what shall be understood by the term ligamentum spirale. Kölliker, by whom the name was given, as well as Löwenberg, include under it the whole semilunar cushion of connective tissue which connects together the external wall of the ductus cochlearis and the capsule of the cochlea. This varies considerably in different species of animals, both in form and size; sometimes it extends far into the scala tympani, especially in the lower turn of the cochlea, sometimes but a little way (figs. 321 and 322). I prefer as Henle also appears to do, to designate by this term only the part of this layer which is triangular in section, and homogeneous in adults, and with which the membrana basilaris is continuous, and which in fact answers to a ligament.

sioned in part by the easily separable nature of the several structures, and especially by the peculiar mode of junction of the two chief types of tissue of the cochlea, the connective tissue and the epithelium; for these are here interwoven with each other in a manner not elsewhere seen in the body.

In axial vertical sections, as in figs. 321 and 322, the crista appears in the form of a hook-like thickening superimposed upon the vestibular side of the lamina spiralis ossea. It is not sharply differentiated from the bony tissue, since the stellate corpuscles of the latter recur in the matrix of the crista, and vascular loops also enter its substance. In some instances, irregularly formed lamellæ of calcareous salts are deposited in it, and in the Bats a tolerably regular kind of ossification occurs. The net of the matrix is either composed of stiff fibres, or is of a more homogeneous nature, and behaves like dense connective tissue to reagents. I think, therefore, that it may be most correctly regarded as an osteogenous substance (in the sense of the term used by Müller and Virchow) developed in continuity with the vestibular periosteum of the lamina spiralis ossea. It may here be provisionally stated that the crista becomes of a somewhat deeper colour than the subjacent bone in perosmic acid and in chloride of palladium.

If the crista be examined from the vestibular surface (figs. 324, 325), the projecting border, in consequence of the presence of deep indentations, appears to be broken up into separate segments of nearly equal size, and of elongated quadrangular form,—the auditory teeth of Huschke (28), which really resemble a row of incisor teeth seen from the anterior surface. Internally, these teeth are prolonged into a number of rounded or elongated, often peculiarly lustrous or highly refracting structures (fig. 325, *d*), which are nothing else than the processes of the osteogenous substance of the crista. The furrows between these, as well as the furrows between the auditory teeth, are filled with small roundish angular cells, which clearly belong to the epithelium of the ductus cochlearis, as Kölliker (30), for a part of it at least, maintains. These cells are continued externally, by means of the interdental furrows, directly into the epithelium of the sulcus spiralis internus (fig. 324),

Fig. 324.

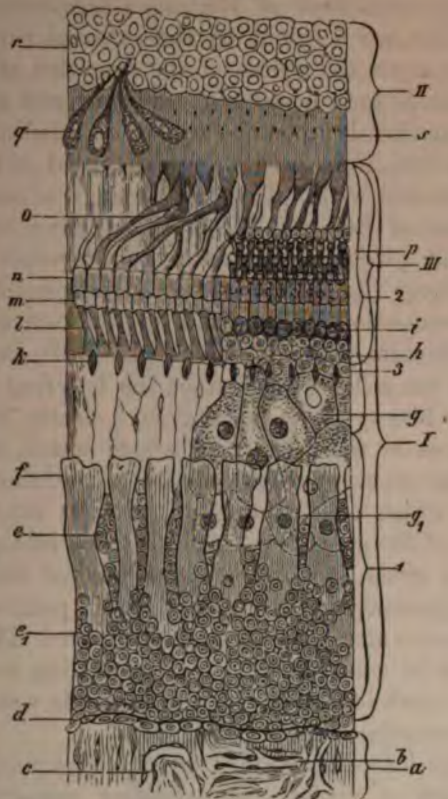

Fig. 324. Tympanal wall of the ductus cochlearis of the Dog. Surface view from the vestibular scala, after removal of the membrane of Reissner, magnified 300 diameters. *I*, Zona denticulata of Corti. *II*, Zona pectinata of Todd and Bowman ; 1, Habenula sulcata of Corti ; 2, Habenula denticulata of Corti ; 3, Habenula perforata of Kölliker. *III*, Organ of Corti ; *a*, part of the lamina spiralis ossea, destitute of epithelium ; *b* and *c*, periosteal bloodvessels ; *d*, line of attachment of the membrane of Reissner ; *e* and e_1, epithelium of the crista spiralis ; *f*, auditory teeth with the interdental furrows ; *g*, g_1, large-celled (swollen) epithelium of the sulcus spiralis internus, partly glimmering through the auditory teeth, removed in the left half of the preparation ; *h*, smaller epithelial cells in the neighbourhood of the inner slope of the roof of the organ of Corti ; *k*, foramina for the nerves ; *i*, internal hair cells ; *l*, internal pillars ; *m*, their capitate extremities ; *o*, external pillars ; *n*, their capitate extremities ;

just as on the other side they pass without interruption into the tympanal epithelium of Reissner's membrane (figs. 321 and 324). They are deficient on the external borders of the teeth, as well as on the apices of the processes of the crista. The membrana tectoria here rests (see below, and figs. 321 and 322, *M t*) immediately upon the osteogenous substance of the crista, but at both these points a few flattened cell rudiments are sometimes met with. Towards the angle of attachment of the membrane of Reissner, the epithelial rows separated by the teeth and processes constantly run together to form a continuous layer (fig. 324, *e* and e_1). Independently of the immediate connection of the cells in question with the remaining epithelium of the ductus, to which Mr. Baer (Student in Medicine) has called attention in the lettering of the preparation, the history of its development clearly demonstrates the correctness of what has been above stated, since in embryoes the ductus everywhere possesses a continuous epithelial investment, which only undergoes apparent interruption in consequence of the great development of the osteogenous substance of the crista, just as the investment of the membrana tectoria is apparently interrupted, whilst in point of fact it is really continuous along the interdental grooves. Thus it comes to pass, that in transverse sections, according to whether a groove or a tooth is struck, the continuity is sometimes preserved and sometimes lost.

The special interest attached to this structure, in a histological point of view, is the peculiar connection of the epithelium with osteogenous substance, which can otherwise be scarcely regarded as an immediate substratum for a true epithelium. The characters of the crista vary to a remarkable extent in the different species of animals. Man, as Löwenberg (39) correctly states, has the flattest, but at the same time the longest crista, and the auditory teeth project but slightly. The Bat appears to possess the relatively

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p, lamina reticularis ; *q*, a few mutilated external hair cells ; *r*, external epithelium of the ductus cochlearis (Claudius's cells of authors), removed at *s*, in order to bring into view the bases of the external hair cells.

strongest, and perhaps also the highest crista, together with extraordinarily sharp teeth, which are curved almost into the form of claws. The height and size diminish in proportion as the cupola is approximated. In regard to the physiological

Fig. 325.

Fig. 325. Crista spiralis, after the removal of all the investing structures. From a woman aged 28. Vestibular surface view. Magnified 300 diameters; *a*, Labium tympanicum of the crista (point of transition into the membrana basilaris, at the botom of the sulcus spiralis internus); *b c*, auditory teeth of the labium vestibulare; below *c*, is the sulcus spiralis internus, as seen in perspective, enclosed by its two labia; *d d*, processes of the crista; *e e*, sections of small processes; *f f*, grooves between the processes, which gradually diminish in depth towards *g*, and are ultimately continuous with the plane of the lamina spiralis ossea; bone corpuscles are indistinctly visible.

significance of this remarkable structure, no opinion has hitherto been formed, except that it constitutes a support to the membrana tectoria.

After the removal of the epithelium in the region of the organ of Corti, the vestibular surface of the membrana basilaris appears to be quite smooth, or presents only a feeble radial striation. The vas spirale, with the fibrous bands of its adventitia, glimmers through the superjacent textures when this part is seen from the tympanal surface.

The vas spirale of Huschke (figs. 323 and 331), sometimes double, is a small vein imbedded like one of the sinuses of the dura mater in the homogeneous matrix of the membrana basilaris (fig. 331). It is connected by means of branches regularly given off (fig. 323) with vessels of the lamina spiralis ossea. More externally we meet, as Breschet observed, and as I can testify in many instances, with another vessel, situated at the root of the ligamentum spirale (fig. 322).

From the points of contact of the bases of the external pillars of Corti onwards (see below), the basilar membrane presents a distinct radial striation (zona pectinata of Todd and Bowman, 54). The striæ are the expression of a thin cuticular lamella, which lies on the vestibular surface of the homogeneous connective-tissue substratum of the membrane, and belongs to the epithelium of the ductus cochlearis. This is particularly well shown in vertical sections (fig. 331), when three layers are distinctly visible. * First, the cuticular layer (*u*), the striation of which I agree with Henle (26) in considering to depend on the presence of fine fibres; then the middle layer (*b*), the principal portion of the basilar membrane, a relatively thick structureless membrane, which passes uninterruptedly into the labium tympanicum of the crista spiralis (fig. 321), and below this, upon the tympanal surface, is a layer of extremely fine connective-tissue fibrils, running for the most part spirally, with delicate fusiform cells (fig. 334), which when seen in transverse section (as in fig. 331), are of course spheroidal, like the sections of the fibres, and give a granular punctated appearance to the mass. The younger the animals the thinner is the middle homogeneous layer, and the thicker the tympanal fibrous layer; this exhibits a greater development also in the first turn of the

* See also the statements of Deiters (13) and Löwenberg (39).

cochlea, at least in Man. These connective-tissue fibres are obviously the remains of the original mucous tissue of the scala.

I am unable to determine whether the membrana basilaris possesses an unusually high degree of elasticity; it does not, at any rate, exhibit a disposition to roll inwards at the edges; it tears easily, and successful transverse sections show that the membrane is always smooth and tense between its two points of attachment.

The parts of the ductus cochlearis hitherto described must be regarded as constituting its proper connective-tissue wall, or membrana propria, under which term I include Reissner's membrane, the innermost layer of the lateral connective-tissue cushion with the stria vascularis, and the ligamentum spirale, the homogeneous layer of the membrana basilaris, and the crista spiralis. An objection can only be raised, perhaps, to the latter, and I may observe in regard to it, that it is easy in the cochleæ of Man, which have been long preserved in glycerine, to detach the crista, together with the membrane of Reissner and the membrana basilaris, from the outer border of the lamina spiralis ossea, and thus to show that it is an integral part of the proper wall of the ductus.

Epithelial Lining of the Ductus Cochlearis. Organ of Corti.

We have already spoken of that part of the epithelium of the cochlea which covers the crista spiralis, the membrane of Reissner, and the outer wall of the ductus; the most important part, however, the epithelium of the membrana basilaris, still remains to be carefully described.

The middle part of the basilar stratum of epithelium forms the *organ of Corti* of Kölliker (figs. 321, 322, *f*—*p*; fig. 324, III; fig. 326), the several parts of which are formed of more or less modified columnar epithelial cells and cuticular formations. The *organ of Corti*, again, is itself (see the sections exhibited in figs. 321 and 331) arranged with lateral symmetry around a centre that at the same time forms a supporting framework—the *arches of Corti*. The arches overhang the membrana basilaris, and are composed of an *internal* and of an *external pillar or rod*. The row of *internal hair cells* (fig. 326, *e*, and fig. 331, *i*) and the granule layer (fig. 331, *h*—*i*), as well as more

internally the epithelium of the sulcus spiralis internus, rest against the internal pillars. The cells of the latter, from the innermost part of the sulcus to the hair cells, become constantly higher.* The hair cells themselves reach the crest of the arch, so that this internal portion of the organ of Corti forms a slope looking inwards from the arches.

The reverse occurs with the external division, which is of somewhat greater breadth, and in various species more or less steeply roofs it in externally. It is composed of the three rows of the *external hair cells*, and of the columnar epithelial cells immediately adjoining them, the *supporting cells* of Hensen, which become progressively shorter until they are continuous with the simple cubic epithelium of the zona pectinata.

Associated with this complex series of cells are still two membranous cuticular formations, the *membrana tectoria* (figs. 321 and 322, *M t*), and the *lamina reticularis* (fig. 331, l—l_1; fig. 326, *D*, surface view).

The *pillars of Corti*, in profile views, have the form of a slender Roman S (sign of integration). The upper enlargement is the "head" or "caput," the lower the "pes" or "foot," and the intermediate rod-like connecting piece is the "body" of the pillar. A peculiar appendage is attached to the head, the "capitular lamina." The inner pillar has two of these, which, however, are continuous with one another; an internal small one, which, when seen in profile, looks almost like a hook (fig. 327, *B g*); but in surface views, and from without, appears indistinctly as a dark crest (fig. 327, *C D g*); and an external large one which, more or less curved, appears as a direct laminar process of the body; this is arched like a hood over the caput, and sometimes, as in Vesperugo (fig. 327, *D*), exhibits a distinct excavation along the external surface. The caput of the inner pillar projects outwards like a pyramid, with a somewhat blunt point (fig. 327, *C D*). The superior (vestibular) margin is slightly prolonged, and at the lateral borders a shallow excavation may also be observed. The basal surface of the in-

* In no adult Mammal does the epithelium fill up this sulcus, though this certainly appears to be the case in embryoes (Kölliker, Hensen), but always forms a single layer as far as to the region of the internal hair cells.

Fig. 326.

Fig. 326. The organ of Corti of the Dog, vestibular surface view, magnified 700 diameters. The membrane of Reissner and the membrana tectoria have been removed. *A*, crista spiralis, in part of a dark colour in consequence of the nerves, which have been stained black by perosmic acid, being seen through it ; *B*, epithelium of the sulcus spiralis internus ; *C*, capitate ends of the rods or pillars of Corti ; *D*, lamina reticularis ; *E*, external epithelium of the membrana basilaris ; *a*, cells of the sulcus spiralis seen indistinctly through the auditory teeth ; *b*, external boundary line of the auditory teeth (the latter, on account of the deeper focussing required, being scarcely perceptible) ; *c*, cuticular meshwork between the internal epithelial cells ; *d*, position of the vas spirale ; *e*, internal hair cells ; *f*, capitula of the internal pillars ; *fi*, capitular laminæ of the internal pillars ; (the opposed capitular laminæ form with higher focussing a clear cuticular roof over the heads of the external pillars, stretching from the internal to the external hair cells ;) *g*, boundary line between the external and internal pillars ; *h*, heads of the external pillars glimmering through the capitular laminæ of the internal pillars ; (each

ternal pillars is nearly rectangular. In profile views the foot appears triangular.

The foot of the external pillar is of considerable size, and is expanded in a fan-like manner on the membrana basilaris. The body is more slender, and the double curvature of the S is much more marked. The caput, in opposition to that of the inner pillar, is bent inwards, and forms, in profile, a segment of a circle somewhat resembling the form presented by a lateral view of the caput astragali.

The caput astragali is, in fact, the object to which the caput of the external pillar may best be compared, except that in this the two lateral surfaces, corresponding to the malleolar articulations of the Talus, are of equal size, whilst the upper surface is not excavated, but moderately convex. Deiters (13) compares it to a boat (heeled over); Löwenberg (39), to the head of a Bird, the beak of which corresponds to the capitular lamina. If we seek for a comparison for the internal pillar, the upper end of the ulna may be accepted as somewhat resembling it. The coronoid process represents the above-described triangular projection of the caput; and if we conceive the olecranon to be somewhat prolonged and arched forwards, it would exactly resemble the external capitular lamina, whilst the dorsal tuberositas olecrani corresponds to the hook *g* (fig. 327, *B*); the lateral groove would also be represented by the sinus lunatus ulnæ.

The capitular lamina of the external pillar arises by means of a long stalk from the middle of the external superior border, and terminates in an oar-like expansion (fig. 327, *A d*). It constitutes, as will be subsequently shown, the first phalanx of the lamina reticularis.

The presence of finely granular cell protoplasm at two points of both sets of pillars, the caput and the foot, is deserving of particular attention (fig. 327, *B c* and γ; fig. 331, *n*

head exhibits as a clear circle the indistinctly seen optic transverse section of the bodies of the external pillars ;) *l*, phalangiform capitular laminæ of the external pillars (first phalanges) ; *k*, first ring with the hairy scales of the first external hair-cells ; *m* and *o*, second and third rings and brushes of hair ; *n* and *p*, second and third phalanges ; *r*, supporting cells of Hensen ; *q*, cuticular meshwork between the epithelial cells (enclosing frames, Schlussrahmen of Deiters).

and *o*). Its existence in the latter situation was, to a certain extent, known to Corti. It appears in the form of a nucleated mass of protoplasm, of various shape, which is firmly connected with the substance of the pillar, and as the history of its development teaches, is nothing but the nucleated remains of some of the cells, from which the pillars are formed. In profile

Fig. 327.

Fig. 327. Isolated pillars, magnified 800 diameters. In all the figures, *a* or α, represents the caput; *b* or β, the body; *c* or γ, the foot of the pillars. *A*, External pillar of Mus musculus, the caput seen half *en face* from above; the capitular lamina provided with a phalangiform end. *B*, Profile view of an internal and external pillar of Mus musculus, in nearly natural position: *f*, capitular lamina of the internal; δ, of the external pillars; *g*, internal uncinate process of the internal capitular lamina; *i*, caput, with clear nuclear-like mass and granular remains of protoplasm; *e*, detached fragment of protoplasm; *c*, nucleus, with remains of protoplasm at the foot of a pillar. *C*, External surface of two internal pillars of the Mus musculus, seen *en face* (lettering as in *B*). *D*, Two internal pillars from the Vesperugo noctula, magnified 600 diameters, in the same aspect. The capitular laminæ exhibit a distinct groove, and at *l*, a fine punctation. The rest of the lettering as before.

views, these cell-remains occupy the acute angle that each pillar makes with the membrana basilaris. It is frequently observable, as Böttcher first stated, (see also Hensen, 27,) that the protoplasmic substance extends upon the membrana basilaris from one pillar to the other (fig. 332, *h*). As remains of this connecting bridge, threads are not unfrequently seen lying on

the membrana basilaris between the pillars, which must not be confounded with nerve fibres (Deiters' system of supporting fibres).

The protoplasmic masses situated near the heads of the pillars have been less known and attended to.* They lie at the outer side of both pillars, and therefore in the concavity of the arch of the inner pillar (fig. 327, *B e*), close under the most projecting part of the caput, and just beneath the origin of the peduncle of the lamina of the outer pillar. In young animals I have sometimes seen a nucleus at this point, of the same form and size as that at the base. After treatment with a 0·05 per cent. solution of chromic acid, a nucleated structure appears near the caput of almost every pillar (fig. 327, *B i*), whilst the surrounding mass appears finely granular, and is continuous with the just-mentioned protoplasmic mass.

After the application of hardening reagents, the bodies and bases of both pillars exhibit a fine but very distinct longitudinal striation, and occasionally it may be seen to be split into fine stiff fibres which are prolonged into the striated lamella of the membrana basilaris. The capitula, on the other hand, always remains homogeneous. I have never seen a cavity either in the bodies or in the bases. The substance of the pillar, as Böttcher first observed, is very resistant; in solution of potash, however, it rapidly undergoes solution, and shrinks to some extent in solutions of neutral salts and of acids. I have found the pillars well preserved in Man twenty-four hours after death. The principal portion of them appears to belong to the cuticular formations, a view that is supported by their connection with the lamina reticularis, which will be described immediately.

The two pillars are so connected as to form a kind of arch, the caput of the external pillar lying in the concavity between the capitular lamina and the caput of the inner pillar (fig. 327, *B*; figs. 331 and 332). The capitular lamina of the internal

* Hensen (27, p. 499) mentions that the protoplasm at the bases of the pillars ascends as far as to the heads, but gives no further details. Perhaps the little laminar appendages of the heads of the internal pillars are referrible to these remains of protoplasm which Max Schultze (50) has described, and which project into the cavity of the arch.

pillar consequently covers the caput and the capitular lamina of the external one, but so that the much longer phalangiform extremity of the latter constantly remains free (fig. 326, *fi* and *l*; fig. 329, *c* and *d*; fig. 334, e_1). As the internal pillars are more numerous, and their capita consequently more slender than the outer ones, it follows that the caput of an external pillar always touches at least two internal pillars, and thus the previously mentioned lateral excavations of the inner capita is produced. Owing to this circumstance, the coupling of the pillars to one another is of a very firm character. The dissimilarity in point of number here leads to the same results as occurs in the ginglymus of the articulation at the elbow; namely, that the occurrence of any lateral displacement of the pillars is prevented. It remains, however, an open question whether a radial articular movement of the capitula of the pillars (around a spiral axis) be possible. I have always observed that the surfaces in contact with one another are flat; such a movement, however, could only occur with coincident bending of the pillars, if the attachment of the bases to the membrana basilaris were fixed, as appears to be the case, especially in regard to the external pillars, the bodies of which often break off, whilst the bases remain adherent.

If the mode of connection of the capitula with one another be carefully considered, it enables us to understand the somewhat complicated markings presented by the vestibular surface of the arches of Corti, when seen *en face* (figs. 326 and 334. A number of spiral and radial lines then make their appearance, of which the spiral are occasioned on the one hand by the internal and external contour lines of the two opposite capitula, and on the other by the external margin of the capitular lamina of the internal pillar (fig. 334), whilst the radial are caused by the contour lines of the capitular laminæ of the several internal pillars, and by the capitular masses and the peduncles of the capitular laminæ of the external pillars, seen indistinctly shining through the former. In regard to this point, I must refer the reader to figs. 326 and 334, which may be combined with the vertical sections exhibited in figs. 331 and 332. A few words may still be added in reference to the internal line of demarcation of the capitular laminæ of the inner pillars. One of these

laminæ projects like a phalanx between every pair of hair cells (see fig. 326). But since the internal hair cells are much broader than the internal pillars, and at the point corresponding to each hair cell a rounded gap occurs in the margin of the capitular lamina, the capitular lamina existing on each of the internal pillars must present a different aspect, according to whether one of these pillars is exactly opposite a hair cell, or is situated between two of them. And thus it occurs that, on isolation of the internal pillars, differently formed internal appendices are seen, which in general, as has been already mentioned, resemble a little hook in profile. (See the careful description given by Deiters, 13.)

By their juxtaposition the opposite pillars overarch a kind of tunnel extending along the whole length of the lamina spiralis, as far almost as to the end of the hamulus. The lumen of the tunnel is triangular on section,* the longest side of which is in general formed by the membrana basilaris, and the shortest by the internal pillars. The smaller the species of animal, the narrower becomes the membrana basilaris; the shorter the pillars, the steeper their rise from the membrana basilaris, and consequently the greater the relative height of the arches; the difference in size between the external and internal pillars then almost entirely disappears. The larger animals have very long pillars, forming an arch of considerable span. Man presents the flattest form of arch, the transverse section resembling a low trapezium. (Compare fig. 321, from Man, with fig. 322, from Vesperugo.) Other peculiarities result from differences in the form of the pillars. In Cheiroptera and Mice they are short and compressed; in Man, slender and strongly arched, as they are also in the Dog and Ox. Man possesses the longest capitular laminæ. The size of the pillars, as well as the height and span of the arches, differs in different parts of the lamina spiralis. As a general rule,

* The term lumen may be used with perfect propriety, since, with the exception of the above-mentioned remains of protoplasm attached to the pillars, the supporting fibrous bands of Deiters on the floor, and the nerve fibres running through the tunnel, only endolymphatic fluid is contained in its interior. (See also Reichert, 44.)

Fig. 328.

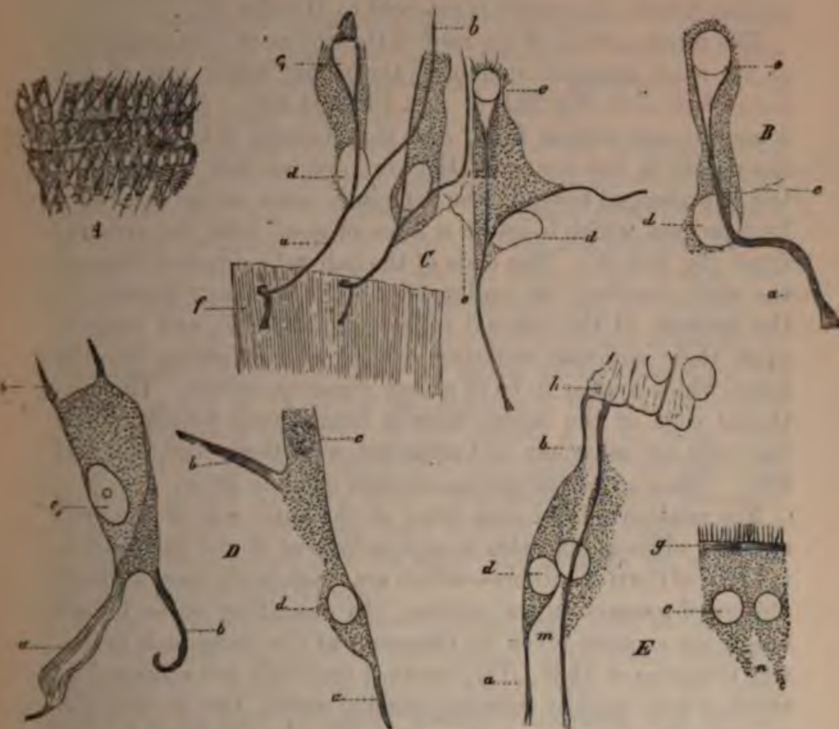

Fig. 328. *A*, from a specimen prepared in chloride of gold, showing the three rows of the external hair cells of the Dog *in situ*, after the removal of the lamina reticularis, and of the membrana basilaris, with the phalangeal and basilar processes, magnified 300 diameters. *B*, External hair cells (twin-cells) of Vesperugo noctula, magnified 800 diameters : *a*, basilar process (the phalangeal process not visible) ; *c*, upper nucleus, with claw ; *d*, lower nucleus ; *e*, fine fibril (nerve). *C*, Three external hair cells still connected with the basilar membrane, from Vesperugo noctula : *a d c e*, as in *B* ; at *c*, some fine hairs are still preserved ; at $c_{,}$, the nucleus is absent, and a conical process, probably a portion of protoplasm, projects beyond it ; *b*, phalangeal process ; *f*, fragment of the membrana basilaris. *D*, Two external hair cells from a woman aged 23, magnified 800 diameters : lettering as before ; *c*, dark spot (? nucleus), the nature of which cannot be determined with certainty ; $c_{,,}$, superior nucleus, with nucleolus which in the hair cells is always remarkably small. The phalangiform process, *b*, of these cells is torn away, and the remains have retracted towards the

these dimensions increase towards the hamulus. (For more precise details the reader is referred to Hensen, 27.).

The inner portion of the roof of the arches of Corti supports, as its most essential structure, the single spiral row of the *inner hair cells* (fig. 331, *i*; figs. 334 and 335). These are of a compressed conical form, and the strongly defined nucleus lies nearly in the centre of the very delicate cell body. This last is prolonged towards the tympanic scala in the form of a long process, which is lost in a layer of small cells, the *granule layer* (fig. 335, *A*). The ends of the hair cells directed towards the scala vestibuli are embraced by the accessory laminæ of the capitula of the internal pillars (fig. 333, *i h*), and support upon their cuticular covering a close pile of strong rod-like hairs, which appear to be of a very resistent nature. The epithelial cells of the sulcus spiralis immediately adjoining the hair cells are columnar, and alternate with them (figs. 326 and 331). They cover the just-mentioned granule layer.

The relations of the cells lying at the outer side of the arch are less obvious, and this is especially true of the hair cells—the cells of Corti of authors—which are amongst the most difficult objects of research in the cochlea. In describing these I shall follow the account given by Gottstein at the Innsbruck Scientific Congress of 1869. The *external hair cells* are arranged in three or four spirally running parallel series, but so that the several cells of each row alternate with great regularity with those of the immediately adjoining rows (fig 326). Each row contains about as many cells as there are external pillars. According to Gottstein, the cells have two nuclei—an upper smaller one, and a second larger one, situated in the lower part of the cell. Two thick processes are given off from the cell body near the lower nucleus; the straight *basal process*, which is firmly attached to the basilar membrane by a small triangular swelling (fig. 328), forming the stronger and longer, and the

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base. *E*, Isolated twin-cones from the Dog, magnified 800 diameters. Two kinds of cells, *m* and *n*, are at first in immediate connection, so that the pointed extremity of *n* runs into the cell protoplasm of *m*, the hairs being directed upwards. The phalangiform processes, *b*, are still in connection with the phalanges, *h* ; *g*, cuticular margin of the rings with hairs ; *a c d*, as before.

phalangeal process, more slender and somewhat curved, which coalesces with a phalanx of the lamina reticularis lying immediately externally and to its side (Gottstein). Moreover, fine short fibrils — *nerve processes* — are not unfrequently seen attached to the cell body (fig. 328).

The basal process runs straight to the cell body, and then divides into two arms, which embrace the upper nucleus like a pair of forceps (fig. 328, *B* and *C*). Viewed *en face*, these claws, as soon as the hairs fall off from the cells, appear indistinctly, like a semicircular area, through the ring of the lamina reticularis into which the upper (vestibular) end of the cells is inserted. Deiters (13) first noticed this area, and although he was already acquainted with the claws, did not give a correct explanation of it. Kölliker (30) appears to have regarded it as a surface view of the cilia, as he* depicts a semicircular line exactly at the point at which the claws glimmer through, and describes it as a circlet of cilia. The cilia, however, here also, as in the inner hair cells, form a thick brush, covering the whole terminal surface of the cells (Middendorp, 40, and figs. 326 and 329 in this Manual).

Careful examination of the external hair cells shows that they are really composed of two stalked cells fused into one; that they are, in fact, true twin or double cells. One of these cells turns its hairy nucleated extremity upwards, and adheres by its peduncle to the membrana basilaris; the other, intimately blended with it, lies (turning spirally round it) at the side of the former, and, in opposition to it, has its nuclear end directed downwards (towards the tympanum), and its peduncle (phalangeal process) upwards. From the fusion of the two conical cells, the above-described doubly stalked and bi-nucleated twin bodies result (fig. 328, *B C D*; fig. 331, *p*). The fusion of the two cells is more or less complete in different animals. In Rodents and Cheiroptera the cells can scarcely be detached from one another without, for the most part, effecting their destruction, the several fragments becoming unrecognisable. In Dogs (fig. 328, *E*) I have occasionally been successful in separating a somewhat mutilated hairy portion from the basal

* Kölliker, *loc. cit.*, fig. 521.

portion and rest of the cell body, which then has the form presented in the figure, and runs out into two peduncles. These two-stalked remains of cells have been described as peculiar cells by Deiters (13) under the name of "hair cells" ("Deiters' cells" of Kölliker). In correspondence with the same character in the internal hair cells, the upper portion of the cells have here also a thick cuticular cover, each of which is received into a ring of the lamina reticularis (see the description of this part), and supports the hairs.

The external slope of the roof of the organ of Corti presents many varieties in different animals. It is worthy of note that in the case of Man there are *four* or perhaps *five* rows of external hair cells (figs. 329 and 334); whilst in all the other animals that I have examined there are only three rows.* The hair cells are moreover of very large size in Man; their processes are thick, and somewhat resemble cell protoplasm, whilst the hairs are very long, and as stiff as bristles. In the embryo, a closely compressed group of columnar cells replaces the hair cells, and these gradually flatten down into the epithelium of the zona pectinata. Each hair cell probably results from the cleavage of a columnar cell; the two portions remaining more or less firmly adherent to one another.

With the exception of the spiral fibrous bands, to be hereafter described in the account of the nerves, no other structures occur between the hair cells. Sufficient notice has already been taken (p. 152) of the columnar supporting cells of Hensen, lying to the outer side of the hair cells (fig. 329, *h*).

A peculiarity that still remains to be mentioned is the abundance of clear brown pigment cells which in Man are especially found in the laminæ of the lamina reticularis, as well as in the epithelium of the ductus cochlearis, and in particular on the stria vascularis. Corti (10, p. 111) has already called attention to them.

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* Hensen (27) remarks, without stating whether in Man or in animals, that in the second or third turn there appear to be "more than four hair cells." Löwenberg depicts (fig. 4) four brushes of hair in a transverse section of the organ of Corti from a child, but says nothing respecting the presence of four rows of hair cells in Man, either in the text or in the explanation of the plates.

The *membrana tectoria of Claudius* (*Corti's membrane*, Kölliker) (figs. 321 and 322, *M t*) commences at the line of attachment of the membrane of Reissner to the crista spiralis as an immeasurably fine lamina. It covers the crista, adhering very intimately to it, and, gradually increasing in thickness, attains its maximum at the sulcus spiralis internus, and terminates (as I agree with Henle and Gottstein in finding), after gradually becoming extremely attenuated, as a thin edge in the neighbourhood of the hair cells. It here closely overlies the whole surface of the organ of Corti, that is to say, of the lamina reticularis. (See below.)

The principal portion of the membrana tectoria appears to be finely striated in a radial direction; but where the membrane rests upon the crista, its under-surface presents an irregularly plexiform perforated appearance (relief of the crista), whilst its outer terminal portion, according to the descriptions of Löwenberg (39) and Henle (26), runs out with a fine plexiform marking, which is, in all probability, occasioned by the projecting brushes of cilia belonging to the external hair cells. The application of additional names to indicate the several zones of the membrane would indeed be superfluous for an organ so overloaded with terms as this of Corti. On the other hand, the consistence of the membrane of Corti is a matter of special interest. I do not know what claim it has to be called an elastic membrane. Fragments of it, when fresh, are perfectly soft; and whatever may be the manipulation to which they are subjected, the edges never exhibit any tendency to curl inwards. After being hardened in alcohol, the membrane undergoes considerable contraction, but preserves on its surface the impressions of structures accidentally adhering to it. Thus I have occasionally found the brushes of hair of the outer hair cells almost imbedded in the substance of the membrane. These have consequently undergone some displacement, and the lamina reticularis, together with the hair cells, have been carried away in addition to the hairs of the latter. These points are not unimportant, and I shall again have occasion to refer to them. It is demonstrable, however, that the membrane of Corti, as Henle (27) alone, so far as I know, has stated, is of rather soft and almost gelatinous consistence.

According to Kölliker (30, 34) and Hensen (27), it is probably to be regarded as a cuticular structure (excretion) formed by the epithelial cells of the crista and of the sulcus spiralis internus. The latter form a thick layer in the embryo, and subsequently atrophy in the same ratio as the membrane of Corti undergoes development. In Birds, as Hasse (20) states, the membrana tectoria is continued, without any sharp line of demarcation, into the mucous mass in which the otoliths of the lagena are imbedded.

The most complicated structure of the ductus cochlearis is unquestionably the *lamina reticularis* of Kölliker, the extremely delicate surface-markings of which I have endeavoured to represent in figs. 326 and 334. This plexiform lamella is composed of a number of annular and finger-biscuit, or digital-phalangeal-like frames, the "*annuli*" or "*rings*" of Böttcher (2), and "*phalanges*" of Deiters (12). The borders of these frames have double contours; and both the so-called annuli and the phalanges can be obtained in an isolated state. Internally to th arches of Corti (see the illustrations of Deiters, 13) we find only *a single* series of phalanges and annuli (see fig. 333, in part according to a preparation made by Gottstein), through which last the cilia of the inner hair cells project. These annuli are sometimes continued into a second incomplete reticular investing structure, which embraces the heads of the immediately adjoining epithelial cells of the sulcus spiralis internus. Externally to the arches of Corti succeed the greater part of the plexiform lamella, and three or four rows of phalanges and annuli, corresponding to the number of the external hair cells. These, again, are continuous, at the outer border of the organ of Corti, with an irregularly formed cuticular meshwork (the "terminal frames" of Deiters), which, like the supporting cells of Hensen, is developed on the vestibular surface of the epithelium of the zona pectinata, and requires no special description. The annuli and phalanges are arranged regularly in alternating order. Each phalanx is surrounded by four rings, and *vice versâ.**

A glance at fig. 326 will sufficiently illustrate the statements

* Strictly speaking, this only holds good if, as will presently be shown, the conception of the phalanges be somewhat extended, and be made to

that have been made. The first row of the external rings begins close to the outer ends of the capitular laminæ of the internal pillars; externally, each phalanx of the second row forms the boundary to each side of the phalangiform terminal piece of the external capitular laminæ (fig. 326, *k, f i, l, n*). The

Fig. 329.

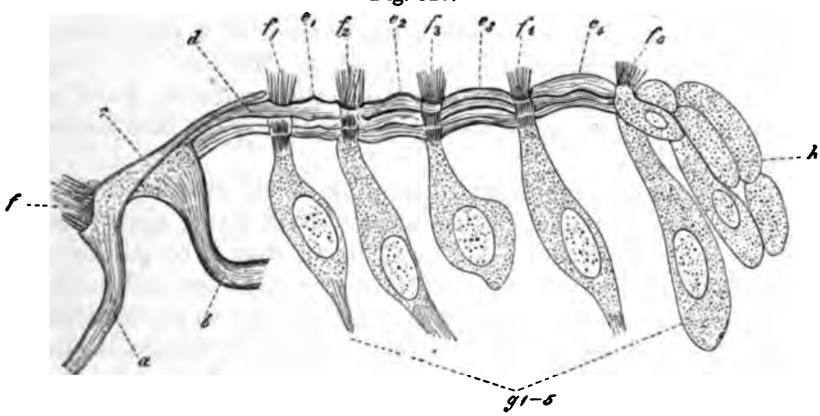

Fig. 329. Fragment of the lamina reticularis of a new-born child, seen in profile, and magnified 800 diameters. *a*, Internal, *b*, external pillar; *c*, capitular lamina of the internal pillar ending in front of the first brush of hairs, f_1; *d*, capitular lamina of the external pillar, with its phalangiform appendage; *f*, hairs of the internal hair cells, the hair cells themselves not preserved; f_1—f_5, five brushes of hair from the external hair cells projecting through the annuli of the lamina rèticularis (in surface views only four rows of brushes of hairs can with certainty be counted, here and there a fifth row may be discovered, appearing as though it had been displaced forward); e_1—e_4, phalanges; g_1—$_5$, external hair cells, mutilated, but still adhering to the lamina reticularis; *h*, supporting cells (Hensen).

terminal portion of the external capitular lamina also participates in completing the circumference of the annuli of the second row. In regard to the completion of the third ring, it need only be remarked that externally the completely de-

include the capitular laminæ of the pillars as well as the terminal frames; otherwise it could only be said in regard to the annuli of the third row in Man, that they are surrounded on all sides by phalanges.

veloped phalanges are deficient (see fig. 326), and thus the terminal frames of Deiters are produced.

Every annulus is occupied with the base of the hair cell belonging to it. The frames of the annuli are continuous with the frames of the adjoining phalanges, so that on isolation of a phalanx or of an annulus, fragments of the adjoining annuli (or phalanges) are always carried away, just as it is impossible to isolate a single mesh of a net without destroying the several adjoining meshes. Moreover, the phalangeal frames are occupied by a delicate membrane, which is nevertheless sometimes destroyed, so that only the bare framework remains.

No similar morphological description of the external surface of the lamina reticularis has hitherto been given, apart from the correct statement made by Kölliker, that it constitutes a cuticular cover to the organ of Corti. A right comprehension of this structure, which at first sight appears so complicated, and at the same time a correct understanding of the arches and organ of Corti, only becomes possible when all these parts are considered in their mutual relations as forming one whole.

If we travel over the organ of Corti, from within outwards, and for the sake of simplicity take that of Man, in whom the hair cells are very numerous, we find six rows of cells arranged one behind the other, and regularly alternating: the internal hair cells, the internal and the external pillars of Corti, and three rows of external hair cells. The regular alternation of their disposition is only disturbed by the varying numbers of the internal hair cells and pillars.

Close examination of the pillars of Corti soon renders it apparent that they correspond in structure to the external hair cells. Each pillar is chiefly composed of a cuticular metamorphosed twin-cell, of which one part, the nucleated basis, is turned towards the membrana basilaris, whilst the other is directed towards the lamina reticularis. The nucleated portion of this last part is situated at the capitular laminæ of the pillars, where we have already (p. 154, *et seq.*) noticed their nucleated protoplasmic remains, whilst they have long been recognized at the bases of the pillars. Moreover, the two processes are present. The basilar process belongs to the upper portion of the proto-

plasmic remains, that is to say, to the upper cells, and forms a portion (the most external cortical portion) of the body of the pillars. The phalangeal process is unquestionably represented by the capitular laminæ. It belongs to the residual mass of protoplasm at the base of the pillars (the inferior cells); and just as the hair cells are fused with the basilar process, so it is blended with the body of the pillars. This is most distinctly seen in the external pillars, but cannot be overlooked even in the internal ones. The history of the development of the pillars, first given by Kölliker, teaches that they are originally conical epithelial cells of the basilar membrane; but that they really result from the fusion of two cells is evidenced by the residual mass of protoplasm at the capitulum and base, each still retaining, in some instances, its own nucleus. We are not, however, at present in a position to decide whether each pillar proceeds from the union of two originally distinct cells, or, as I consider occurs in the case of the external hair cells, from the fission of one cell with subsequent cuticular metamorphosis of the product of the division.* Each of the external hair cells corresponds, as is obvious from its position, sloped obliquely outwards, to a ring, with the phalanx adjoining it externally. Each phalanx is the cuticular tunic of a hair cell, which lies beneath and is firmly attached to it, just as a tortoise is covered by its shell, and thrusts its head through a ring of bone. Thus the fact is explained that the external phalanges become shorter, and the terminal ones appear as irregular terminal frames, whilst the outermost row of hair cells is less sloped. Long slightly inclined hair cells, as in the Cat, Ox, and Man, furnish a broad lamina reticularis, with elongated meshes; whilst steep short hair cells, as in Cheiroptera, have a slender narrow reticular plate, with short broad meshes.

If we put aside the several peculiarities of the internal hair cells, it will be seen that the apparently complicated structure

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* In accordance with the foregoing account, the capitulum of the pillars corresponds to the cilia-bearing extremity of the hair cells. Gottstein and I have long entertained this view, based on our researches, that rudiments of cilia exist on the capitula of the pillars (see, for example, fig. 334). The fibrous structure of the pillars is also suggestive of the same fact.

of the organ of Corti is formed upon a simple plan. Several rows of columnar (twin) cells are regularly arranged, one behind the other, upon a broad zone of the lamina spiralis, and are firmly maintained in position between two membranous (cuticular) boundaries (the lamina reticularis and the lamina striata of the membrana basilaris.) A pair of these columnar twin-cells, the pillar cells, are in great part also cuticularly metamorphosed, establishing a firm supporting arch for the whole. The cuticular investing lamella proceeds from the capitular pieces of the arch, and is developed from the ends of the cells. It is gradually lost towards both sides in layers that become progressively thinner upon the internal and external epithelium. Divergences from this plan are caused by the inner hair cells, which occasionally do not occur as double cells, and moreover, like the internal pillars, do not correspond in number to the outer hair cells. The internal pillars appear to form the middle point of the whole system, whilst, both internally and externally, they take part in the formation of the lamina reticularis.

The careful mode of attachment of the external hair cells is deserving of special notice. They are immoveably fixed, and appear as though they were immoveably extended, by means of their two processes and their capitular pieces, between the lamina reticularis and the basilar membrane. These cells, together with the pillars of Corti, constitute the distinguishing peculiarity of the cochlea of Man and Mammals. I shall again have occasion to refer to the hair cells, in speaking of the mode of termination of the nerves.

The apparatus to which the terminal fibres of the nervus acusticus are distributed is thus constructed, and in the essential parts of this, the two kinds of hair cells, they actually end. I shall preface their description by a few words in regard to the general relations of the trunk of the auditory nerve.

THE AUDITORY NERVE, AND ITS RELATIONS TO THE ORGAN OF CORTI.

According to the statements of Stieda (51—53), which I shall here for the most part follow, the auditory nerve arises

by two roots from the medulla oblongata. One of these is composed of delicate fibres, and its ganglionic nucleus of origin (central auditory nucleus of Stieda) consists of small ganglionic masses in the floor of the fourth ventricle. The second root, which, according to Stieda, contains remarkably thick axis-cylinders—thicker than those of any other nerve—arises from a special large-celled ganglion of origin situated in the crus cerebelli ad medullam oblongatum (lateral auditory nucleus of Stieda). Deiters (16) also has described and depicted this nucleus, without, however, recognizing the origin of the auditory nerve from its ganglion cells. Further details, together with the literature of the subject, will be found in Stieda's treatises (*loc. cit.*). The thick-fibred root, like a posterior root of a spinal nerve, has a small ganglion upon it soon after its emergence from the medulla.

The two roots speedily coalesce to form a common trunk, the primitive fibres of which were not unfrequently observed by Czermak (11) to divide and branch, and are probably to be regarded as fasciculi of primitive fibrils, possessing only medullary sheaths, (II. 2, vol. i., p. 158, of this work,) since it is impossible to demonstrate the presence of the sheath of Schwann in them. In the internal auditory meatus the trunk divides into two branches, the ramus vestibularis and the ramus cochlearis. The former again presents a small ganglion, the *intumescentia gangliformis* of Scarpa, and breaks up into the rami ampullares and reticularis, and the ramus sacculi. The much stronger ramus cochlearis also gives a small fasciculus to the septum membranaceum utriculi et sacculi (Henle, 26), and to the macula cribrosa quarta of Reichert (45), which, however, is contested by Middendorp (40), and then passes through the tractus spiralis foraminulentus directly to the first turn of the lamina spiralis and the modiolus, from whence it gives off branches to the remaining coils of the spiral lamina. Before, however, the fasciculi of fibres enter the lamina spiralis, the branches collectively traverse the ganglion spirale, occupying the canalis ganglionaris at the base of the lamina spiralis. Probably a bipolar ganglion cell is here intercalated in the course of each nerve fibre. Numerous ganglion cells are similarly interposed in the principal trunks, as well as in the ramus vestibularis,

appearing in the form of nucleated enlargements of the axis-cylinder. (See fig. 26, *B*, p. 173, vol. i.)

Proceeding onwards from the ganglion, the fibres, which are still always strongly medullated, form a flat plexiform expansion (the anastomoses and communications being very frequent) (fig. 330), which lies between the tympanal and vestibular lamina of the lamina spiralis ossea, though much nearer to the former. The anastomoses between the coarser and finer fasciculi may here be distinguished. The latter (fig. 330, *b*) are very numerous in Man, just before the entrance of the nerves

Fig. 330.

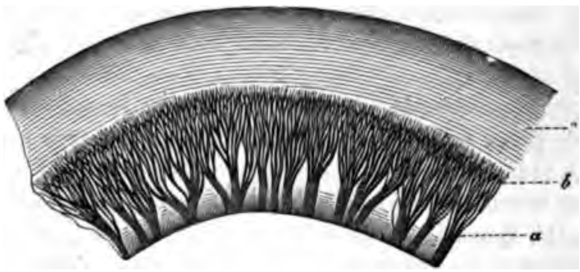

Fig. 330. Lamina spiralis in the first turn of the cochlea, seen from the tympanal surface, from a child aged one year and a half, showing the expansion of the nervus cochlearis. *a*, Large trunk, with numerous anastomoses; *b*, zone-like terminal series of fine anastomoses; *c*, membrana basilaris. Magnified 30 diameters.

into the ductus cochlearis, so that in consequence a delicate dentated line appears in surface views. The several terminal fasciculi of the nerves quickly become attenuated, whilst the fibres lose the greatest part of their medullary sheaths, and pass through fine canals of the membrana basilaris into the cavity of the ductus cochlearis.

The minute and in general circular canals for the nerves are of measurable length in the upper turn of the cochlea, since they traverse the membrana basilaris obliquely; and even anastomoses are observable between the several pale nerve fibres during their passage. In the lower turn, on the other hand, their course is more vertical. In surface views the holes are seen to be, in Man, small, round, and in close proximity; but they are larger, and of elliptic form, in the Dog

Fig. 331. Vertical section of the organ of Corti in the Dog, magnified 800 diameters. *a*—*b*, Homogeneous layer of the membrana basilaris; *u*, its vestibular layer, corresponding to the striæ of the zona pectinata; *v*, tympanal layer, with nuclei, granular cell protoplasm, and intervening sections of fibrils of connective tissue; *a*, labium tympanicum of the crista spiralis; a_1, continuation of the tympanal periosteum of the lamina spiralis ossea; *c*, thickened commencement of the membrana basilaris immediately external to the passage of the nerves, *h*; *d*, vas spirale; *e*, bloodvessel; *f*, nerve fasciculi; *g*, epithelium of the sulcus spiralis internus (not well preserved); *i*, an internal hair cell; *k*, its basal process; surrounding the latter, above the point of emergence of the nerves, are a few nuclei and a finely granular mass into which the nerve fibres stream (granule layer); *l*, inner part of the capitular lamina of the internal pillar and hairs of the internal hair cell; *m*, capitula of the two pillars joined together,—the body of the external pillar, to which the above belongs, cut through its middle; behind it the body and base, *o*, of the next pillar comes into view; *n*, base with nucleated remains of protoplasm of the internal pillar; *p*, *q*, *r*, three external hair cells (only traces of the hairs preserved), the first one alone complete, of the two others only the heads are seen; *t*, basal portion of two other hair cells; *z*, Hensen's supporting cells; *l*—*l*, lamina reticularis; *w*, a nerve fibre passing to the first hair cell, *p*, which can be followed beneath the arch to the point of emergence of the nerves.

Fig. 331.

and in other animals (fig. 324, *K*). Löwenberg gives full details respecting them. See also Kölliker, *Mikroskopische Anatomie*, p. 751.

The pale fibres which have traversed the foramina still continue to pursue their radial course, in order to reach their terminal organs, and must be divided into two groups, the *internal* and *external terminal nerve fibres*, corresponding to their connection with the internal and external hair cells. Both the internal and the external fibres traverse, immediately after their emergence, a thin layer of small roundish cells, the *granule layer* (figs. 331 and 335 A), which is situated upon the internal slope of the organ of Corti, close to the point where the nerves traverse it. I shall again recur to the consideration of this granule layer, as well as to its relations to the nerve fibres, when I come to describe the spiral fibrous bands of the organ of Corti, and now proceed to follow out the radial nerve fibres to their destinations.

The inner radial fibres, as I have on several occasions been able to observe (fig. 335 B), pass directly through the granule layer, and are at once continuous with the pointed extremities of the internal hair cells. These fibres, as far as I can see, have a relatively considerable thickness (1·5—2 μ), and I am therefore disposed to regard them not as isolated axis-fibrils, but as a fasciculus of such fibrils, that is to say, as an axis-cylinder. (See vol. i., pp. 157, 158.) In regard to their diameter, they may well correspond to the undivided axis-cylinder of a medullated auditory fibre entering at the foramina nervina. Hasse (18—25) everywhere found a similar mode of termination of the nerves in the hair cells of the Bird and Frog. (See *infra.*)

The external radial fibres, as Gottstein has noticed, pass between each couple of the internal pillars into the tunnel of Corti, traversing it at about the middle of the height of the pillars, so that they resemble stretched harpstrings when seen in profile. In like manner they leave the cavity of the arch between the external pillars, and pass, rising a little towards the vestibule, directly to the external hair cells, with which they coalesce (figs. 331 and 332). In Dogs and Bats I have on several occasions seen this mode of termination of the

nerves in the most satisfactory manner; at least, as regards the innermost row of hair cells. The same mode of termination may, however, be also admitted for the other rows, since several fibres may frequently be seen to pass together between the external pillars.

The external radial fibres appear to me to be constantly far

Fig. 332.

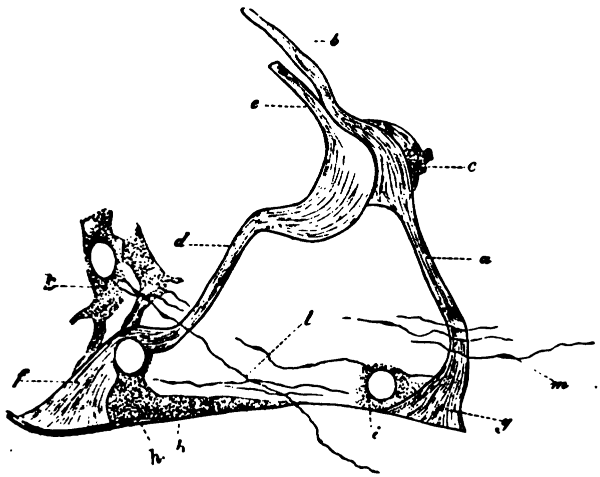

Fig. 332. An arch of Corti (from a woman thirty years of age), prepared with needles, and magnified 610 diameters. (The natural disposition of the parts as seen in sections is not preserved.) *a*, Internal pillars; *b*, its capitular lamina; *c*, appendage, probably a portion of an internal hair cell; *d*, external pillar; *e*, capitular portion (only partially preserved); *f*, its base; *g*, base of the internal pillar; *h*, nucleus, with its protoplasm stretching far in between the two pillars; *i*, nucleus at the base of the internal pillar; *k*, rudiments of two external hair cells; *l*, *m*, fragments of radially running and distinctly varicose fibres which may in part be followed to the external hair cells (nerve fibres).

more delicate than the internal. In perfectly fresh specimens they exactly resemble the finest axial fibrils of the retina, described by Max Schultze, with the same characteristic drop-like varicosities that these present as they run to the rod-granules. I have observed this particularly clearly in an osmic-acid preparation made by Gottstein. Max Schultze (50), as is well known,

gave the first description of such pale nerve fibrils from the cochlea; and I am inclined to regard as external radial fibres all those extremely fine varicose fibrils which are met with in the sulcus spiralis internus, in addition to the thicker fibres going to the internal hair cells, even if, as in fig. 333, they apparently pass to the internal hair cells, as they must all pursue this direction. The same applies to the fine fibres seen in fig. 335 A, which run upwards in the granule layer, and between the internal hair cells; for, as above mentioned, those fibres which I distinctly saw terminating in the internal hair cells are far thicker. The varicosities of the external radial fibres (see also fig. 17, p. 148, vol. i.) cannot be mistaken for anything else; and whoever has but once seen these varicose nerve fibrils of the cochlea, will not readily confound them with connective-tissue fibrils. Unquestionably we do here and there see small granule-like enlargements in tolerably regular sequence in the extremely delicate connective-tissue fibrils of the tympanal surface of the basilar membrane, but these never have the peculiar lustre and exquisite drop-like form of the true nerve varicosities. With regard to these two peculiarities, as well as to the circumstance that the drops assume a blackish tint when macerated in perosmic acid, I might suggest that the true nerve varicosities are the expression of an extremely delicate medullary sheath, which would thus not be absent in the primitive fibrils of Max Schultze—my axis fibrils. Hasse, on the other hand, denies the existence of a medullary sheath in the thick terminal nerve fibrils of the Bird and Frog, but admits the presence of a delicate sheath of Schwann after their entrance into the ductus cochlearis. I have not been able to make any observations favourable to this view, either in Birds or in Mammals.

The nervous nature of the radial fibres just described, and their termination in the internal and external hair cells, may now, I believe, after the repeated observations made by Gottstein and myself, be accepted as a fact, in our knowledge of the cochlea. I am convinced that no one who works with a good method can deny its truth. The question may, however, be reasonably asked, whether other nervous elements—and I refer in particular to the *spiral fibrous bands* of Max Schultze—do not also occur in the cochlea?

Fig. 333.

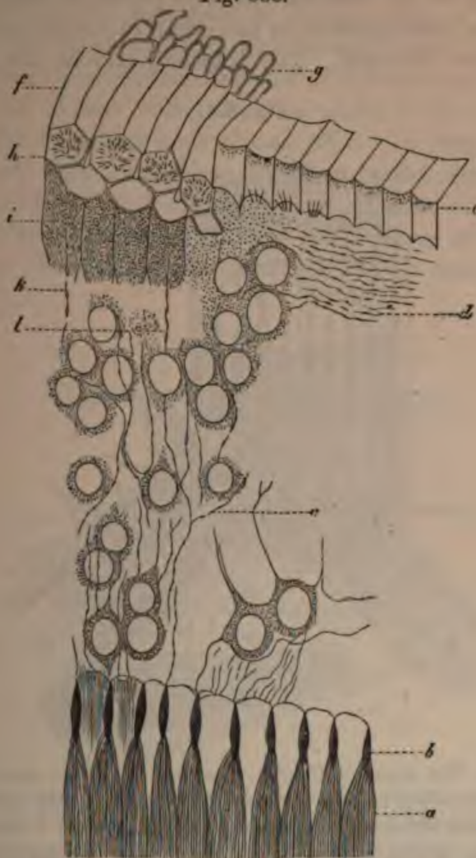

Fig. 333. Auditory granule layer of the Dog, with the parts adjoining. The lettering corresponds to two specimens, from one of which the part extending from *f* to *l* was taken. The commencement of the arch of Corti, together with the internal hair cells, is here much displaced outwards; the granule layer has been considerably teazed out. Magnified 610 diameters. *a*, Fasciculi of nerves represented diagrammatically; *b*, foramina nervina; *c*, granule cells, with processes and intervening fine fibrils, which in part run to the foramina for the passage of the nerves; *d*, spiral band of fibres upon the inner hair cells, curving, as it would appear, in part from the radial fibrils; *e*, heads of the internal pillars; *g*, commencement of the lamina reticularis; *h*, hairs of the internal hair cells; *i f*, capitular laminæ of the internal pillars; *k l*, distinctly varicose nerve fibrils becoming lost at the level of the internal hair cells.

According to my observations, two principal bands of spiral fibres can be distinguished in the organ of Corti: *one internal* and the *other external.* The internal, and at the same time

Fig. 334.

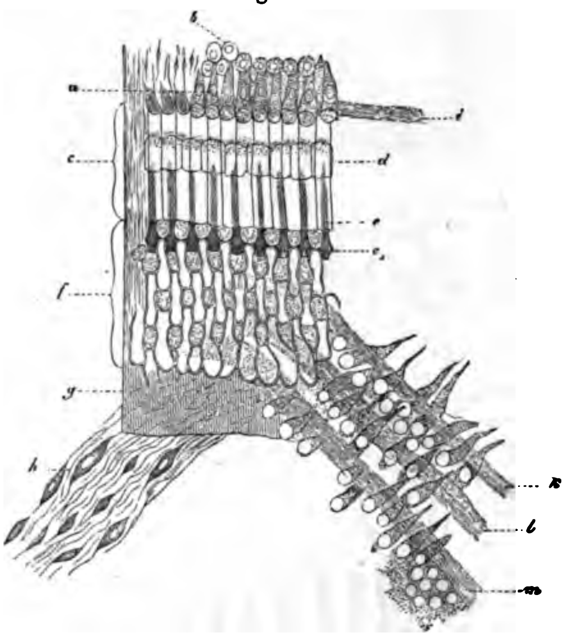

Fig. 334. The organ of Corti. A surface view of a specimen prepared with needles, from a woman aged 28, showing the spiral bands, and magnified 400 diameters. *a*, Internal hair cells; *b*, small round cells of the sulcus spiralis internus; *c*, capitular portions of the pillars of Corti; *d*, small punctiform formations upon the latter; *e*, capitular lamina of an external pillar glimmering through the capitular lamina of the internal, and becoming continuous with the first phalanx, e_1; *f*, lamina reticularis, withfour rows of hair rings and four rows of phalanges, which are continuous with large laminæ (Deiters' terminal frames); *g*, membrana basilaris; *i*, internal spiral fibrous band; *k l m*, three external spiral fibrous bands, with intervening external hair cells; *h*, connective tissue with fusiform cells of the tympanal surface of the membrana basilaris.

the smallest band (fig. 334, *i;* fig. 335 A, *c*), corresponds to the series of the inner hair cells, and runs beneath the lamina reticularis along the lower ends of these cells. The external band

consists properly of three parallel divisions, which correspond to the three rows of hair cells, in the interspaces of which it runs upon the same plane as the internal band. The innermost division runs between the row of the external pillars and the first row of hair cells; the two others in the intervening spaces of the following rows of hair cells. In Man (fig. 334) I have hitherto only seen three divisions of the external band, notwithstanding that here more rows of cells occur, and as Löwenberg has already stated, the spiral fibres are here most easily seen. Very frequently (see fig. 334), in teazed-out spe-

Fig. 335 A.

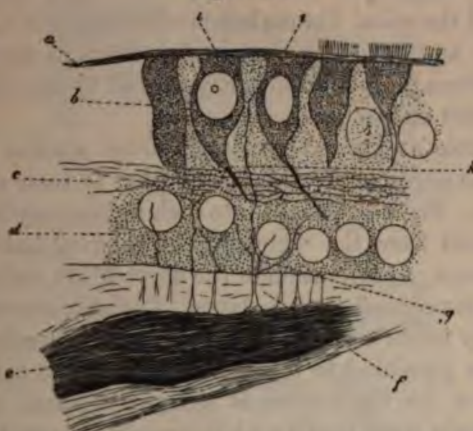

Fig. 335 A and B. Two longitudinal sections (spiral sections) of the organ of Corti through the region of the internal hair cells. From the Vesperugo noctula. Magnified 800 diameters.

A *a*, Cuticula (section of the internal division of the lamina reticularis); *b*, internal hair cells, of which two possess long somewhat shrivelled processes; *c*, spiral fibres; *d*, granule layer; *e*, nerve fasciculi (oblique section); *f*, a few traversing nerve fibres; *g*, one such fibre dividing in the granule layer into several fibrils; *h*, a longer finer fibre running outwards between the hair cells.

cimens, we obtain the hair cells still firmly cleaving to the fibrous bands between which they lie; as yet, however, I have not been fortunate enough to discover any connection existing between the fibres and the cells.

The fibrils of the spiral bands belong to the most delicate

structures known in histology. With low powers they appear, as Hensen (27) has already indicated, when he compares them with the molecular layer of the retina, as a finely granular mass resembling a finely fibrous neuroglia. With very high powers they exhibit extremely small and irregular varicosities, which correspond rather to the granular swellings I have already described as occurring in the finest connective-tissue fibrils, and are clearly different from the delicate drop-like varicosities of the radial primitive nerve fibrils. I desire to call particular attention to this difference between the spiral fibres and outer radial terminal nerve fibres, as it is seen both in fresh preparations and in those preserved in perosmic acid. That I have actually had the spiral fibrous bands of the organ of Corti under observation, and have not confounded them in any way with tympanal fibres, will be sufficiently proved by the illustrations numbered 334 and 335A.

I am unable at present to decide from whence the spiral bands of the organ of Corti arise, or what is their nature and significance. The best insight into their nature may be expected to be obtained from the region of the internal hair cells, this being the point of perforation of the nerve fibres, and seat of the previously mentioned granule layer. Preparations of these unquestionably important parts, teazed out with needles, give the appearances presented in fig. 333. Between the hair cells and the foramina for the nerves is a layer of small round cells with relatively large nuclei and extremely delicate protoplasm, which is seldom preserved in an uninjured condition. These cells, which I have provisionally designated granule cells ("Korn zellen"), give off processes in various directions that in all respects resemble the fibrils of the spiral bands, and appear also (at *d*) to curve round into these bands.* In longitudinal sections of the lamina spiralis (fig. 335A) the elements of the region of the internal hair cells succeed one another in five consecutive layers; the nerve fibres (*e*); the granule layer

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* Fig. 333 is unfortunately not sufficiently good to show the delicacy of the spiral fibres in question, and their difference from the likewise imperfectly represented varicose nerve fibrils which I have represented as taken from another preparation at *k* and *l* in the figure.

(*d*); the spiral fibrous layer (*c*); the processes of the internal hair cells (*b*), which lie between the fibres of this layer as in a network of threads; and lastly, the hair-bearing cuticle (*a*). The nerve fibres are seen entering the granule layer in the form of larger (*g*) and smaller (*f*) fasciculi of axis fibrils. I have also, as at *g*, seen some of the stronger fasciculi of fibrils undergo division. Some of the slender nerve fibrils run upwards between the hair cells, and these, after what has been already stated in page 173 *et seq.*, must be regarded as external radial

Fig. 335B.

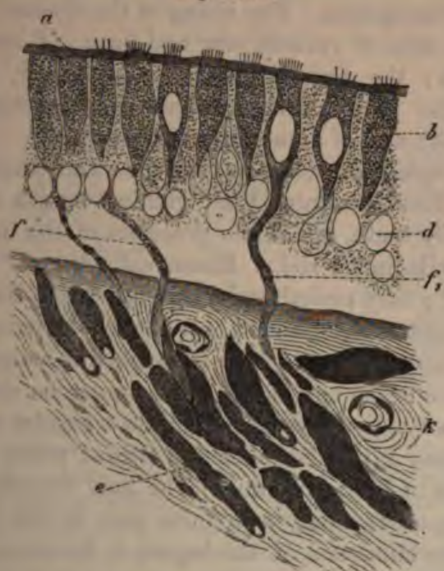

Fig. 335B. *a b d e*, As in the previous figure; *g*, perforating nerve fibre; *f*, similar fibre becoming fused with a hair cell; *k*, transversely divided bloodvessel.

fibres, which are only passing through between the internal hair cells and the pillars. Whether there are yet other nerve fibrils continuous with the processes of the granule cells,—which either indirectly through these, or directly, as Max Schultze (50) and Deiters (13) admit, are continuous with spiral fibres, or curve round into the latter, so that these last must be regarded as

primitive nerve fibrils,*—I am unable to determine. I limit myself here to the simple facts, so far as I can represent them. I shall again have occasion to refer to the significance of the spiral-fibre system.

COCHLEA OF BIRDS AND AMPHIBIA.

The cochlea of Birds presents a simple structure when compared with that of Mammals. In it we find a membrana basilaris extended between two cartilaginous rods, whilst the roof of the ductus cochlearis is formed by the already described tegmentum vasculosum. The lining of the ductus is composed of epithelial cells of various size and form; of hair cells, and granule cells; the two latter forms, however, being only present at the points where nerves pass through the wall of the cochlea; and of a membrana tectoria.

The large epithelial cells are very clear and transparent, and of columnar form, attaining their greatest length upon the so-called auditory teeth, which are processes of the inferior quadrangular cartilaginous rod. Hasse calls them "tooth-cells" (Zahn-zellen); they probably, he thinks, secrete the membrana tectoria. This last is expanded over the whole region of the hair cells, but is never adherent. In the lagena it assumes the characters of a mucous membrane, with numerous otoliths in its interior. Its tympanal surface exhibits a regular mosaic, from the impressions of the hair cells, the cilia of which project into the substance of the membrane. The hair cells themselves, as in Mammals, occupy only a definite zone in the body of the cochlea. The blind end of the lagena is, however, completely filled with them.

Each hair cell is surrounded by a circle or crown of clear columnar epithelial cells—the tooth cells of Hasse; it is of

* Max Schultze. According to a written communication, of which, owing to the kindness of the author, I can take advantage, this observer rests his statements respecting the direct bending round of the here non-medullated auditory fibres into the spiral fibrous bands essentially upon a series of specimens prepared from the human subject. He compares this spirally running layer of non-medullated nerve fibres with the optic fibre layer of the retina, into which the medullated optic fibres similarly and immediately curve round.

columnar form, slightly ventricose below, and prolonged into a long process. The upper extremity supports a large brush of fine stiff hairs, which are of considerable length. Deiters (14) and Hasse (20) admit, as Leydig (36) also did at an earlier date, the presence of only a single strong and long hair upon the terminal surface of the cells, instead of the brush or tuft of hairs, and still adhere to this unquestionably erroneous view, notwithstanding that some of their own observations show that this apparently solid hair exhibits traces of a division into separate filaments. In accordance with this they name

Fig. 336.

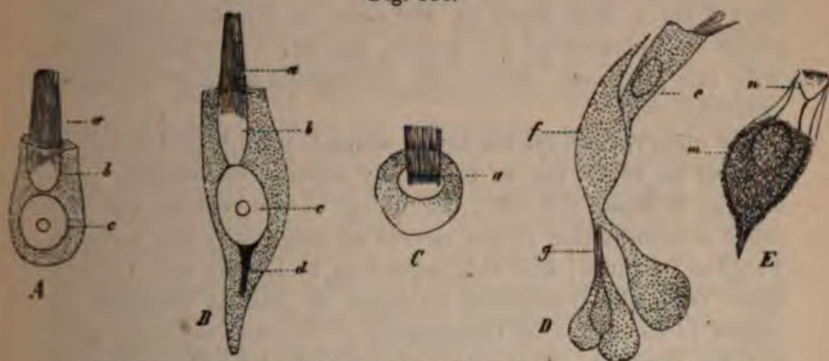

Fig. 336. Isolated cells from the cochlea of a Pigeon, magnified 800 diameters. Fresh specimens, with the addition of 0·5 per cent. solution of common salt. *A B C*, Hair cells; *A* and *B*, profile view; *C*, view of the terminal surface; *a*, tuft of hairs; *b*, clear cup-like spot; *c*, nucleus, with nucleolus; *d*, basal process, with dark fibres extending to the nucleus; *D*, a group of small cell-like structures, *g*, connected by stalk-like processes to a tooth cell, *f*; *e*, hair cell; *E*, tegmental cell; *m*, dark granulated and nucleated cell body, with clear extremity, *n*.

the structures in question "rod cells," a term that I shall exchange for "hair cells," in consequence of the close resemblance they exhibit to the internal hair cells of Mammals. In surface views the hair tuft appears to project from a cup-like depression of the cells, and to extend inwardly as far as to the nucleus. The upper (free) extremity of the cell presents a cuticular hem or border. I have sometimes seen a fine thread extend from the nucleus to the basilar process of the cell.

Hasse depicts a similar appearance in Frogs, and in the hair cells of the arches of Corti in the Bird, except that here the dark line extends from the cell nucleus to the free surface. Hasse (18—24) made the first precise observations in regard to the termination of the nerves in the cochlea, by demonstrating that both in Birds and Frogs the undivided non-medullated nerve fibres pass directly into the basilar process of the hair cells. I am able to corroborate his statements from my own preparations of the cochlea of the Pigeon, where the same relations are found as in the internal hair cells of Mammals (fig. 335B). The granule cells are also present in Birds; they form a thin layer at the base of the hair cells, just above the entrance of the nerves, and are likewise connected with fine processes. Hasse (21, 22) regards them as mutilated epithelial cells.

My observations on the lower animals have been too few in number to allow me to make any definite statements. According to Hasse (22—25), the lining of the cochlea and the mode of termination of the nerves are essentially the same in Frogs as in Birds; and this, according to Leydig and Deiters, apart from the insufficient evidence at present obtained in regard to the mode of termination of the nerves, holds good also for Reptiles. Structures corresponding to the pillars of Corti, the external hair cells, and the lamina reticularis, as I have already had occasion to observe, do not occur in any other class besides the Mammalia.

Comparative Anatomical and Physiological Observations.

On anatomical grounds alone it is evident that the hair cells constitute the essential portion of the cochlea. It must be noted that the hair cells of Amphibia, Reptiles, and Birds rather resemble the inner hair cells of Mammals in their structure and position, in which last the introduction of the arches of Corti and the outer hair cells constitutes quite new features, attaining their highest expression and development in Man. Just as Hasse has demonstrated in the case of Birds and Batrachia, undivided axis-cylinders, forming the termi-

nations of the nerves, run to the internal hair cells in Mammals. The internal hair cells do not form double cells, and are not attached in the peculiar mode of the external. Whether special structures corresponding to the tooth cells (Zahn zellen) of Hasse, exist between them in Mammals, as sometimes appears to be the case in longitudinal sections of the lamina spiralis, must still be regarded as doubtful. The arches of Corti, there can be little question, are essentially a supporting apparatus for the hair cells.

The membrana tectoria and the otolith masses demand closer investigation. Hasse (20—24) has associated the two structures together, as an apparatus specially adapted for propagating vibrations excited from without to the terminations of the nerves lying in close proximity with the cilia of the hair cells; they thus constitute the essential sensation-exciting arrangement of the internal ear, a function that has long been attributed to the otoliths. I am disposed to attribute to these structures a not less important but still directly opposite function, that, namely, of *damping* vibrations. Helmholtz (Ton-empfindungen, etc.,) has shown that a very perfect damping mechanism must exist in the apparatus of the internal ear, and I am of opinion that no constituent of the labyrinth is better adapted to act in this way, by virtue of its anatomical construction and of its position, than the membrana tectoria and the otoliths. The latter are for the most part aggregates of small crystals, destitute of any definite arrangement, but suspended in a mucous substance, which is itself in contact with the auditory hairs. Even the large simple otoliths of the Fish and of other animals are essentially accumulations of smaller crystals. It will be conceded that an apparatus of this nature, which calls to mind a "sand sac," cannot in any way occasion regular vibrations, but is much better adapted to deaden the vibrations of other bodies with which it is in contact. In favour of this view is the observation made by Hensen (73), that the Decapoda, to some extent, make use of certain quartz granules or uric-acid crystals, brought into their vicinity, to supply the place of these otoliths, when lost during each act of moulting. The mucous consistence of the membrana tectoria, to which attention has already been called, its

completely free position as a gelatinous screen or veil (Gallertschleier) over those terminal portions of the terminal auditory apparatus which bear the hair cells, are also, it appears to me, much more in accordance with the view of its being a damper, than of its acting in the manner maintained by Hasse.

Comparison between the Organ of Corti and the Retina.

We are easily led to institute a comparison from a morphological point of view, between the two sensorial apparatuses that are specifically adapted to transfer regularly recurring vibrations to the extremities of the nerves.

The comparison appears so much the more appropriate since the works of Stricker, Schenk, Török and others, quoted below, show that genetically there is no essential difference between the *vesicles of the labyrinth* and the primary *eye vesicle*, whilst both proceed, in the Batrachia at least, from the same germinal lamina—the Epiblast or sensorial lamina. Our knowledge of the process of development is doubtless insufficient to permit of a complete and detailed comparison between the two; what is already known on this subject, however, taken into consideration with our knowledge of the mature organ, supplies the means for drawing a parallel, which I shall here briefly endeavour to give.

No one will question that the sclera and osseous cochlear capsule correspond to each other, and I would just notice the formations of bone that occur in the sclera of the Bird, and of cartilage in the sclera of the Batrachia, etc. The connective-tissue wall of the ductus cochlearis is comparable with the choroid coat, and consequently the scalæ represent greatly developed perichoroideal spaces (see p. 141). The lamina fusca of the sclera is also represented, since both the periosteum of the cochlear wall and the central delicate portion of the external connective-tissue cushion (*e*, figs. 321 and 322) contain similar large branched pigment cells. The corpus ciliare is evidently represented by the stria vascularis, which indeed, in Birds, presents in the tegmentum vasculosum exactly the same structures as we meet with in the processus ciliares.

In order to carry the comparison further, it must be borne in mind that in the eye an involution of the primary eye vesicle takes place, so that this acquires the form of a cup, the foot of which is represented by the optic nerve, and the walls of which, owing to the fact of their being constituted by an involution, are necessarily double.*

* Kölliker (62), p. 276.

The two lamellæ of the cup-shaped secondary eye vesicle thus originating, and the mouth of which looks forwards, are continuous with one another at the border of the cup, the outer lamella being continuous with the optic nerve; the internal lamella alone forms the lining of the cup, and develops into the retina, whilst the external forms the tapetum nigrum. A similar involution is commenced, but is not completed, in the ductus cochlearis. If we conceive such an involution as occurs in the primary eye vesicle to be checked very soon after it had begun, the appearance presented would be that of a vesicle flattened on the side of the involution, and this in section would resemble the sections of the ductus cochlearis marked e_3 and e_4, fig. 320. The flattened side, or that on which the involution has commenced (corresponding to tympanal in the figure), would be that which develops into the retina; the cavity of the vesicle would correspond to that space between the bacillar layer and the pigment epithelium, which at a later period, when the involution has proceeded to its fullest extent, altogether disappears, whilst all the rest of the wall of the vesicle that is not included in the flattened portion would correspond to the flattened or short columnar epithelium of the tapetum nigrum of the choroid. Of course the portion of the wall corresponding to the tapetum is continuous all round with the flattened and thickened portion corresponding to the retina, inasmuch as they are both parts of the walls of the same vesicle. The relations of the parts are precisely similar in the ductus cochlearis. Its internal cavity corresponds to the cavity of the primary eye vesicle; instead of the involution at one spot, we have the innermost layer of its wall (that is to say, the layer originating from the hypoblast, and corresponding to the wall of the primary eye vesicle) undergoing development into a nerve cushion, the auditory nerve apparatus (organ of Corti), which, instead of a disk-like form, has that of a girdle or zone-like lamina, and the innermost layer of cells of which (the hair cells) pass continuously into the remaining epithelial lining of the duct.

Even in matters of histological detail the homology between the retina and the organ of Corti still holds good. The epithelium contains here, as in the cells of the tapetum nigrum, granular pigment, which, however, is of somewhat lighter colour in the ductus cochlearis, and in Man these pigment granules, as has been already mentioned, are found even in the lamina reticularis. For further details I would refer to the transverse section in fig. 335A. I consider the bacillar layer, as well as the external granule layer of the retina, to be represented by the hair cells in the organ of Corti. The cilia are the analogues of the outer segments of the rods, whilst the protoplasmic bodies of the hair cells are the analogues of the soft internal segments, or rod and cone

granules. In the retina it is evident that differentiation has been carried to a greater extent at this point; the rods may therefore be the analogues of the external hair cells, and the cones of the internal hair cells. At any rate, the relations of the nerves indicate something of this kind, for we find that relatively thick fasciculi of axis-fibrils run to the inner hair cells just as they do to the cones, whilst to the outer hair cells, as to the retinal rods, only fine individual fibrils run. Whether any physiological differences also exist between the internal and the external hair cells, as Max Schultze has demonstrated in the case of the rods and cones, may be fairly suspected. The thick cuticle of the lamina reticularis is without homologue in the retina, unless we compare it with the limitans externa, against which view serious objections might at present be raised.

The spiral fibrous bands (*c*, fig. 335A) of the organ of Corti are obviously analogous to the intergranule layer, and the auditory granule layer (*d*) to the internal granule layer of the retina; at least, the entire microscopic relations of these two strata are for the most part similar. The ganglion-cell layer, represented by the ganglion spirale, is in the case of the ductus cochlearis removed to some distance from the preceding structures, and there is consequently a less marked homology with the molecular layer of the retina, which, perhaps, we may consider to be represented by the fine plexiform connective tissue which surrounds the auditory fibres from the ganglion to the entrance into the foramina nervina.

In comparing the two structures together collectively, it must be borne in mind that the elements of the retina are for the most part arranged perpendicularly to one another, whilst those of the organ of Corti, so far at least as regards the group of the external hair cells, are arranged upon the same plane, like those of the retina at the yellow spot.

Structures corresponding to the lens and the vitreous humour cannot be looked for. I am quite aware how incomplete this comparison must for the present remain. I have, however, been desirous to sketch it, since, by prolonged researches in this direction—though doubtless morphological and physiological identity are often far apart—we may expect to obtain some important knowledge to aid in the comprehension of the auditory labyrinth.

Controverted Points; Historical Notices.

In view of the differing statements of various observers already given, we must here limit ourselves to the consideration of such

points as appear to us to be of importance. It is not the object of this work to give in full detail all the innumerable opinions that, just as in the case of the retina, have been advanced on every point of structure in the cochlea.

In the first place, it must be mentioned that Deiters (13), Löwenberg (37—39) and Henle (26) consider that the *membrana tectoria* is firmly attached to the outer wall of the ductus cochlearis, in close proximity to the ligamentum spirale accessorium. Gottstein and myself have never seen anything of the kind in many excellent sections of the cochlea prepared in gelatine; nor have Kolliker (30), Middendorp (40), and Rosenberg (49). Moreover, the drawings of Löwenberg and Henle do not coincide with one another; the fourth cochlear canal of Löwenberg ("canal que j'ai dècouvert," Löwenberg), Henle's "upper chamber," must consequently be given up. Deiters (13) and Henle (26) have given the most detailed description of the crista spiralis. The former represents the small epithelial cells as connective tissue. Hensen (27), with whom Kölliker (30) and Middendorp (40) are inclined to agree, considers the matrix of the crista, which I have described as osteoid substance, to be an epithelial excretion. The connection of the warts of the crista with the teeth was first demonstrated by Henle (26), who also pointed out the tubercle-like thickenings on the tympanal surface of the membrana basilaris. Of the two forms of the *lamina reticularis* described by Henle (26), I am only able to recognize the second as normal; his first one results from the breaking up of the second. The lamina reticularis is always best seen in perfectly fresh specimens.

Henle (26) has also described two different forms of the internal pillars, in reference to which I must express myself in favour of the contrary statements of Middendorp (40). The latter, however, maintains with Deiters (13) that the pillars are hollow; actual transverse sections, which have frequently come under my observation, both in Gôttstein's and my own preparations, prove them to be completely solid structures, appearing as if composed of fasciculi of fibres. In opposition to the statement lately reiterated by Kölliker (30), that the external pillars form varicosities, I can only say positively that I have never observed such appearances under any circumstances, nor is this at the present time a matter of any moment.

Löwenberg describes processes at the lower end of the *internal hair cells*, which branch and communicate with the processes of the granule cells. I have not, however, been able to see them.

Deiters (13) has supplied the most exact description of the *external hair cells*. All subsequent investigators of the cochlea of Mammals have

been apparently surpassed in the examination of this difficult object by that distinguished inquirer. The explanation of the external hair cells given by Gottstein, and here reproduced, differs from that of Deiters in the circumstance that the latter admits the presence of two completely distinct cell forms, which are only connected with each other by thin processes in the external slope of the organ of Corti. One of them bearing hairs (the "rod cells," Stäbchenzelle, of Deiters) is directly continuous with the basilar process ("connecting-stalk," verbindungstiel, of Deiters) and is firmly inserted into the rings of the lamina reticularis. Between the rod cells are found also quite *independent* fusiform cells ("hair cells" of Deiters; "Deiters' cells" of Kölliker, 30) the upper process of which is continuous with a phalanx, and the lower with the connecting stalk of a rod cell. With Gottstein, I am unable to recognize the fusiform cells of Deiters as perfectly distinct structures from the hair cells; in particular the semi-diagrammatic representations contained in the manuals of Kölliker and Frey (fig. 512, for example, and fig. 571) are by no means well adapted to give a correct representation of the true relations of these parts. I always found that each pair of conical cells are united to form a double body. The so-called "cells of Deiters" of authors may be compared morphologically with Hasse's tooth cells of the Bird (see *loc. cit.* 21, Taf. 27, fig. 8), but are here fused in a peculiar manner with the hair cells.

The differences between authors are most numerous in their descriptions of the relations of the *cochlear nerves;* for there is scarcely any conceivable mode of nerve termination that has not been discovered here. Apart from the terminal loops of R. Wagner and Harliss (17), and of the passage of all, or at least of several, nerve fasciculi over the tympanal surface of the membrana basilaris (Corti (10), Böttcher (2), Max Schultze (50), Deiters (18)), views that would not probably receive the support of those by whom they were advanced, all observers now hold the correctness of the statements made by Kölliker (33) and Max Schultze (50), to the effect that the nerve fibres enter into the ductus cochlearis through foramina of the membrana basilaris, and there run either exclusively in a radial direction (Rosenberg (49), Böttcher (30), Middendorp (40)), or in a radiating as well as in a spiral direction (Max Schultze (50), Kölliker (30), Deiters (18), Hensen (27), Löwenberg (39)). All observers are thus in accord in respect to the existence of radiating nerve fibres. Nevertheless only a few positive statements corroborated by drawings exist in regard to their mode of termination, and these alone can be here taken into consideration, since it is impossible to mention all the opinions unsupported by facts—by Böttcher, Rosenberg, Middendorp,

and very recently by v. Winiwarter (57). These are apart from the interesting discoveries of Hasse in the cochlea of the Bird and Frog (see p. 182), the only positive statements hitherto made upon the terminations of the radial nerves in the cochlea. Böttcher has reiterated his opinion, expressed in 1859, that the nerves, after their passage through the habenula perforata, are partly continuous with the cells lying upon the internal series of rods, and partly pass under the arches, and run transversely through to the cell rows of Corti. How far there is here a definitive mode of termination is not, unfortunately, distinctly stated in the extracts to which I alone had access, and we must wait for the appearance of the promised more extended work of Böttcher.

E. Rosenberg described only the mode of termination in the internal hair cells, but upon the whole correctly, and he was the first to give a drawing of these relations. He certainly forgot to mention that his drawing was in great part diagrammatical, for I cannot suppress a doubt in regard to the existence of any preparation corresponding to his fig. 3, Pl. ii. Any one who is even moderately familiar with the hair cells, the cells in the sulcus spiralis internus, and the arches of Corti, will readily admit this.

Middendorp, on the other hand, only recognizes the internal radial fibres, which he considers enter into connection with the cells of the auditory granule layer, and then terminate by free extremities between the internal hair cells.

v. Winiwarter, like Rosenberg and Gottstein (74), saw the previously described termination of the external radial fibres in the outer hair cells, but there are no remarks in his provisional communication in regard to the relations of the nerves to the internal hair cells.

Max Schultze (50) was the discoverer of the *spiral fibrous bands* of the cochlea, and his statements were soon corroborated by Deiters (13), Kölliker (30), Hensen (27), and Löwenberg (39), by the first two of whom they were described in fullest detail. All these authors agree with Max Schultze (see p. 180) in regarding them as of a nervous nature. No one, however, besides this discoverer has advanced any positive statement in reference to the mode in which these cochlear fibres terminate. According to his rather provisional communication (50), the spiral nerve fibres enter into connection with the protoplasmic remains at the base of the internal pillars, and likewise with the cells which are situated at the apices of the arches, presumably also with the external hair cells. Deiters (13), Löwenberg (39), and Kölliker (30), describe, besides the bands which I have also shown to be present, spiral fibres *within* the arches of Corti.

According to the statements of Max Schultze (50), spiral fibres are found there also.

These spiral fasciculi of fibrils unquestionably form the most obscure point in the anatomy of the cochlea. In my opinion, they must be regarded in connection with the small layer of large nucleated delicate cells in the sulcus spiralis internus, which I have pointed out as analogous to the inner granule layer of the retina, and for which I have suggested the name of auditory granule layer (see fig. 385A). As many different views are admissible for this layer and also for the spiral fibres, as are still held for the internal granule layer of the retina, or for the granule layer of the cortex of the cerebellum (see Waldeyer, 75). Thus, in point of fact, Max Schultze (50), Deiters (18), (for a part of them,) and Middendorp (40), have maintained their connection with the nerve fibrils, regarding them as small (bipolar) ganglion cells; whilst Deiters (18) again (in regard to the majôrity of them), as well as Rosenberg (49), and Hasse (21), deny the nervous nature of all of these structures. The statement made by Rosenberg (49) is worthy of notice, to the effect that their number is greater in young animals, which Gottstein has been able to corroborate in the case of young Dogs. Hasse (21) found this also to be the case in Birds. This last-named author (24, p. 409,) denies the existence of any connection of the structures between the hair cells and subjacent tissues, and the nerve fibres.

The results of my own observations in regard to the cells and fibres in question, and upon the mode in which the nerve fibres terminate, do not render it very probable that either the granule cells or the spiral fibres are of a nervous nature. We should in that case have to admit a double mode of termination to the nerves. The difference between the well-established radial *nerve* fibres and the spiral *fibrous* bands (see p. 176 *et seq.*) is also opposed to it. It only remains, therefore, to regard these fibres and cells as a delicate *neuroglia*, and to compare them with the non-nervous elements of the internal granule layer and the intergranule layer of the retina. Positive conclusions, however, can only be drawn from further careful inquiry, especially based upon embryological research.

The older literature of the cochlea is given with tolerable completeness in the work of Hildebrandt-Weber (4th Edit., Band iv., p. 7), and this may be compared with Deiters' Essay (18). Putting aside some discoveries of Huschke (28), the histology of the cochlea dates from the researches of Corti (10), (giving an account of the external hair cells, ganglion spirale, stria vascularis, membrane of Corti, etc.). Very important essays, which first rendered a correct understanding of the morphology of the cochlea possible, were furnished by Reissner (46),

(describing the membrana Reissneri, ductus cochlearis); by Hensen (27), (who described the canalis reuniens, the cæcal origin and termination of the ductus cochlearis, the cell clusters in the sulcus spiralis internus, and many other points); and by Kölliker (30—34), in his embryological researches, in which he demonstrated the development of the organ of Corti from epithelial cells, and gave an account of the lamina reticularis (which he discovered simultaneously with Max Schultze), of the secondary formation of the scalæ, and the passage of the nerves through the spaces of the habenula perforata. Max Schultze (50) also made important statements in regard to the spiral fibres, the granule cell layer, the basal processes of the external hair cells, and the prolongation of the auditory fibres in the form of non-medullated primitive fibrils into the organ of Corti, etc. Deiters (12—15) furnished valuable information upon the internal hair cells, and gave the first exact description of the external hair cells, and of the lamina reticularis, as well as many details respecting almost all parts of the cochlea, the accuracy of which is demonstrated by every good preparation. The account given by Deiters is unquestionably the standard by which all recent investigation into the cochlea must be measured. We are indebted to Reichert (45) for a description of other special points, as the cæcal sac of the vestibule, and for excellent morphological descriptions of the cochlea, and in particular of the ductus cochlearis; whilst Böttcher (1—4) has pointed out the dissimilarity in point of numbers between the internal and external pillars, which he described with extraordinary precision, as well as their arched form, both of which he gave coincidently in point of time with Claudius. Böttcher moreover appears to have been the first to see the granule cells in the sulcus spiralis, though he gave no precise description of them. Claudius published the first histological statements in regard to the cochlea of the Bird. I beg to refer the reader to the text for the recent statements of Henle (26), Middendorp (40), Löwenberg (39), Kölliker (30), and Rosenberg (49).

Our knowledge of the comparative histology of the cochlea rests, apart from the scattered observations of Leydig (36), (in which, however, may be found the first notice of hair cells,) chiefly, and indeed at present almost exclusively, upon the fundamental works of Deiters (14, 15) and Hasse (18—25), which essentially completed the older descriptions of Windischmann and others. We must here also mention the comparative anatomical investigations of Hyrtl (29), and of Claudius (7—9).

In regard to the development of the cochlea, I would call attention to

the works quoted at the end of this note under the numbers 58—65, with which are to be classed the communications of Huschke (28), Reissner (46, 47), Kölliker (34), Hensen (27), Hasse (21), Böttcher (4), Rosenberg (49), and Middendorp (40). A few points have been mentioned in the text, but a continuous account of the development of the cochlea can scarcely be at present given.

METHOD OF INVESTIGATION.—It is unnecessary that I should again recommend the investigation of the cochlea to be undertaken whilst perfectly fresh in the aqueous humour. Equally good results, or even still better, on account of the somewhat greater sharpness of the contours, are obtained from the employment of perosmic acid, which I can recommend as being just as good for the cochlea as for the retina. It can be used in the form of solution, containing from one-tenth to one per cent. The former strength is the best for recent preparations, torn with needles ; the latter for hardening specimens. Solutions of common salt, varying from one quarter to one half per cent., are also very serviceable for preparations teazed out with needles. The pillars of Corti can best be isolated in solutions of chromic acid, containing 0·05 per cent., in which also the hair cells are well preserved. Chloride of gold may be applied with advantage in solution in the proportion recommended by Cohnheim for the cornea, as well as nitrate of silver in one per cent. solution, the latter being especially well adapted for the spiral fibres. I would recommend the following plan for the preparation of good sections. As much osseous substance as possible should be removed from *large* cochleæ with cutting pliers, and two or three small openings should be made into this cavity ; smaller cochleæ should be allowed to remain unopened. The cochleæ must then be macerated for twenty-four hours in a proportionately large quantity of solution of chloride of palladium, containing 0·001 per cent., or of perosmic acid, containing 0·2 per cent. (for smaller cochleæ) or 0·5—1 per cent. (for larger). The specimens are then placed in absolute alcohol for twenty-four hours, or they may be immersed at once in the decalcifying fluid. The best decalcifying fluid is chloride of palladium (0·001 per cent.), with one-tenth part of hydrochloric acid, or one-fourth one per cent of chromic acid. After the process of decalcification is completed, the cochleæ must be washed with absolute alcohol, and then imbedded in fresh spinal cord or in liver. For large cochleæ, a corresponding piece can easily be cut from the latter. The specimen, with its enclosing material, is once more placed in absolute alcohol. As hardening proceeds, the latter contracts so firmly upon the cochlea that this lies immoveably in position, and can be conveniently divided into the finest sections. The cavities of the cochlea may be filled

prior to the imbedding with glycerine and gum, in equal parts, or with a mixture of oil and wax. (See this Manual, p. 1, General methods of investigation, by Stricker, and Klebs, 76.) I consider the gum and glycerine to be unquestionably superior; though in my experience it is quite superfluous to fill the cavities at all, or at most only with the object of preserving the layer of Corti's membrane. My best preparations, from which the above illustrations are taken, were made from cochleæ that had not been filled. Sharp knives are alone required.

Measurements.

The subjoined table contains the most important measurements of the several parts of the internal ear in Man. I have everywhere given round numbers, since the table is only intended to supply general data. For the sake of comparison a few measurements of the corresponding parts in the Dog and Vesperugo have been added. In computing the numbers of the pillars and hair cells, the length of the lamina spiralis was estimated at thirty millimeters. All the measurements, with the exception of No. 2, are given in micromillimeters.

Name of the part.	Observer.	Man.	Dog.	Vesperugo.	Remarks
1. Canalis reuniens, length	Hensen	700			
Can. reun., diameter.	"	220			Narrowest point.
Can. reun., thickness of the walls . . .	"	15			
2. Lamina spiralis membranacea, total length in two adult men . .	Waldeyer	28 or 31 Mm.			In the neighbourhood of the organ of Corti.
3. Ductus cochlearis, width from the commencement of the crista spiralis to the lig. spirale, 1st turn .	"	800	700	360—400	
2nd turn.	"	700	700	350	
4. Ductus cochlearis, greatest height, 1st turn .	"	500	400—450	400	
2nd turn.	"	500	350	260	
5. Length of the Reissnerian Membrane, 1st turn .	"	900			
2nd turn .	"	700			
6. Width of crista spiralis . . . 1st turn .	"	300	150	140—150	
2nd turn .	"	200—250			
7. Length of the auditory teeth	Henle	30			
Breadth	"	12			
8. Sulcus spiralis internus, greatest height .	Waldeyer	60—70	60—70	100—120	

Name of the part.	Observer.	Man.	Dog.	Vesperugo.	Remarks.
9. Distance between the basis of the pillars of Corti	WALDEYER	66—70	80—90	40	In hardened sections between the 1st & 2nd turn.
10. Height of the arches at centre	,,	12	40	21—24	
11. Length of the internal pillars measured on their dorsal surface from the foot to the apex of the arch . .	,,	50	60—70	45	Sections measured in hardened specimens. The accessory lamina is completely omitted in this measurement.
12. Length of the outer pillars taken in the same manner . . .	,,	60—66	90	50	
13. Thickness of the bodies of the pillars, inner .	,,	4·5	90	50	From the new-born child; the length is to a certain extent approximatively given, since the determination of the point of attachment of the process is arbitrary
outer .	,,	3	90	50	
14. Cell bodies of the inner hair cells, length .	,,	18	90	50	
breadth .	,,	6—9	90	50	
15. External hair cells, total length with	,,	48		45	The process is about half the length.
basilar process . .	,,	6—7			
breadth .	,,	4		6—7, 5	
16. Length of the cilia .					
17. Phalanges, average length.	,,	15			
18. Rings, average diameter	,,	6			
19. Epithelium of the membrane of Reissner, thickness . . .	,,	9			
20. Thickness of the epithelium in the sulcus spiralis ext. .	,,	15			
21. Greatest (radial) breadth of the membrana tectoria . . .	,,	200—230			
Greatest thickness .	,,	50			
22. Nuclei of the granule cells	,,	3·5—4·5			
23. Ganglion cells of the ganglion spirale . .	KÖLLIKER	24—35			
24. Number of the foramina nervina . . .	WALDEYER	3,000			In the first turn there are about 110 to one millimeter; at the hamulus about 80.
25. Number of the internal pillars . . .	,,	6,000			
26. Number of the external pillars . . .	,,	4,500			
27. Number of the internal hair cells . .	,,	3,300			
28. Number of the external hair cells .	,,	18,000			In each row 4,500, as many as there are external pillars

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CHAPTER XXXV.

THE OLFACTORY ORGAN.

By PROFESSOR BABUCHIN.

THREE parts must be distinguished in the organ of smell. (*a*) The apparatus for receiving the impressions of odours; (*b*) the conducting apparatus; and (*c*) the central organ to which the odorous impressions are carried by the conducting apparatus.

The first, and a part also of the second apparatus are imbedded in the mucous membrane which, amongst the higher animals, covers the uppermost and the deepest parts of the nasal cavities; whilst in some of the lower Vertebrata (naked Amphibia) it extends as a kind of elevation on this or that wall of the simple nasal passage; and in others, as in Fishes, forms manifold but regularly arranged folds rising from the floor of the olfactory furrows, between or on which the odour-perceiving elements occur. It is impossible to give here an elaborate description of all the peculiarities of the external modifications of the olfactory organ in all animals; this rather belongs to the domain of comparative anatomy. Our duty is to furnish an account of the physiologically active elements of this organ, and their different relations to one another.

The mucous membrane which contains the odour-perceiving elements, presents certain peculiarities, by means of which it can be distinguished, even with the naked eye, from the rest of the nervous mucous membrane. It either possesses a yellowish colour, as in Man, the Sheep and Calf, or is of a brownish tint, as in the Guinea-pig, Rabbit, Dog, and other Mammals. On this account the term *locus luteus* has been applied to it. But inasmuch as this spot is not characterized in all animals by a peculiar colour, another name, the *regio olfactoria*, is perhaps preferable, which, however, only indicates that part of

the nasal mucous membrane where the olfactory nerves branch and terminate. Were it, however, desired to indicate the peculiarity of this spot by a feature characterizing it throughout the whole of the Vertebrata, it would be not so much its colour, but its greater thickness, softness, and, so to speak, greater succulency, as compared with the rest of the membrane. Even this, however, varies in degree in different animals; for whilst

Fig. 337.

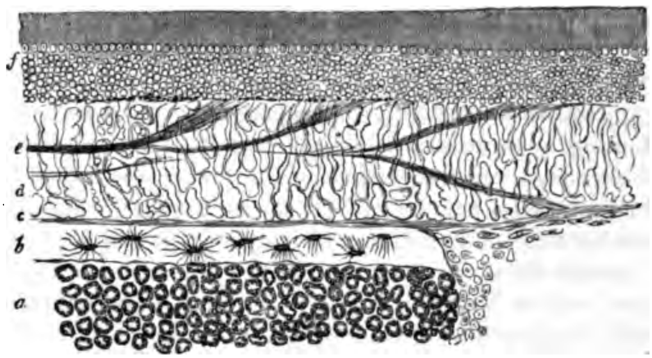

Fig. 337. Vertical section of the septum nasi of the Guinea-pig. The specimen was prepared by maceration in solution of chloride of gold. *a*, Medullary tissue of bone; *b*, osseous lamina; *c*, periosteum; *d*, gland layer, not filled up, that it may be more distinctly seen; *e*, branches of the olfactory nerves; *f*, epithelial layer.

in Birds, for example, the membrane is tolerably dense at this part, and scarcely presents any peculiarity recognizable to the naked eye, in the Plagiostomata it is so soft as to resemble thick mucus.

The works of Todd and Bowman (1), Eckhardt (2), Ecker (3), and others, certainly contributed much to our knowledge of the structure of the olfactory region; but the first really accurate information was furnished by the extremely careful investigations of Schultze, and future research, though it may possibly affect points of detail, will not shake the essential facts that he discovered. Some attempts have, however, been made, with this object in view.

An idea of the general relations of the olfactory region may best be obtained from fine vertical sections carried

through the whole thickness of the membrane, and these, I think, may best be made in specimens of the membrane which have been hardened in solutions of chloride of gold whilst still adherent to the bones. The various structures are thus retained in their normal position, and appear sharply defined. In fine sections of a nasal septum thus prepared from the Guinea-pig, we find that the osseous portion of the septum is invested by periosteum, which is immediately covered by a thick layer of numerous and closely arranged glands (fig. 337). These glands, named the "glands of

Fig. 338.

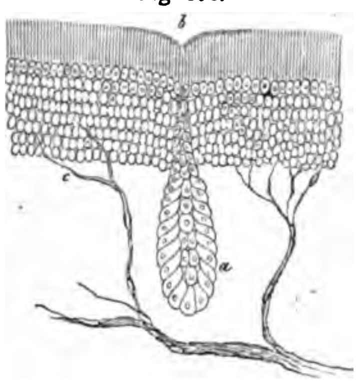

Fig. 338. Section of the olfactory mucous membrane of the Frog. *a*, Gland of Bowman; *b*, its orifice; *c*, fasciculus of nerve fibrils which run between the epithelial cells.

Bowman" by Kölliker, are elongated tubes, which, according to the species of animal, are sometimes simple and more flask-shaped than tubular; and at others are multiform, and characterized by pullulations, and by the sinuous course of their blind extremities. Hence it rarely occurs, as the adjoining woodcuts show, that, in vertical sections of the membrane of the higher animals, any simple gland can be followed throughout its whole length; in general, only transverse sections of the several parts, at different heights, are seen. Better preparations are obtained from the lower animals. The glands contain an epithelium, which at the fundus consists of large granular, nearly spherical cells, which in some animals have yellowish

or brownish pigment in their interior. Chloride of gold stains them of a deep black colour. Towards the excretory duct the epithelium assumes a more polygonal form, and becomes less granular. The excretory ducts finally reach the surface between the elements of the next following external layer (fig. 338). The orifice sometimes opens at the bottom of a funnel-shaped depression of the membrane. Amongst the lower animals, as in the Frog, it may be very easily demonstrated that the excretory duct is lined, from its commencement to its termination on the surface of the mucous membrane, with smaller cells. Immediately in front of the orifice slender epithelial cells are situated, which are elongated in the direction of the axis of the excretory duct.

At the point where the olfactory region passes into the ordinary mucous membrane, the glands become fewer in number, and ultimately vanish altogether, being replaced by the ordinary mucous glands. According to Kölliker, even in the olfactory region of the human subject, instead of the just-described glands, we meet only with the ordinary mucous glands. Schultze, however, considers that in Man they properly constitute a transitional form, and resemble in appearance Meibomian glands.*

In Fishes, the glands are entirely absent, but are replaced by numerous cells.

The glands are separated from one another by ordinary connective tissue, which is continuous on the one hand with the periosteum, and on the other extends as far as to the epithelium. I have not been able to discover the basement membrane described by Hoffman. The appearance of a membrane is caused by the contour line of the connective tissue in contact with the epithelium. Both here and in the deeper layers of the connective tissue are many fusiform cells provided with processes, and especially in the lower animals, containing black pigment. M. Schultze has also observed free masses of pigment, as well as pigment cells, in the higher animals. Lastly, imbedded in the connective tissue are vessels and the ramifica-

* More recently, Schultze (5) has observed acinous mucous glands in the olfactory region of Man.

tions of the olfactory nerves, which come out with remarkable distinctness in specimens prepared with chloride of gold.

The superficial layer of the olfactory mucous membrane is an epithelium which in specimens prepared with chloride of gold (as is shown in fig. 337) is divisible into two, an external, which

Fig. 339.

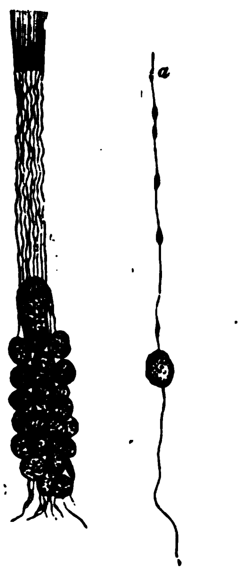

Fig. 340.

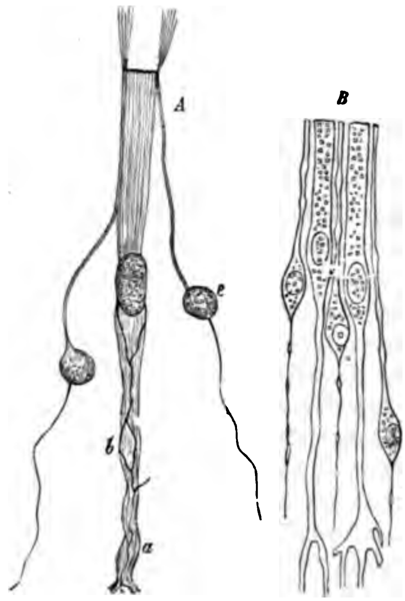

Fig. 339. A group of olfactory cells from the Proteus, with an epithelial cell lying within them. From a specimen prepared with Müller's fluid. *a*. An isolated olfactory cell, after treatment with a diluted solution of sulphuric acid.

Fig. 340. *A a*, Epithelial cells from the olfactory region of the Proteus (from a specimen prepared with Müller's fluid); *d*, the processes apparently connected with them; *c*, olfactory cells. *B*, Epithelial and olfactory cells from Man; after Max Schultze.

is finely striated transversely, and an internal granular layer. It was formerly considered to be a laminated epithelial layer. Eckhardt and Ecker to some extent indicated its nature correctly, but we are indebted to the beautiful researches of Max Schultze for the full details of its structure. From these it

appears that the epithelial portion of the olfactory organ is constructed upon one and the same type in all Vertebrata, so that the description of its structure in any one animal is applicable to all. We shall therefore select an animal whose epithelial cells are large and easily isolable, as the Proteus, in which the histological elements attain an almost colossal size, and have nevertheless been as yet but little examined. If now the entire olfactory organ of a Proteus be macerated for a day in Müller's fluid, then be transferred for the same space of time to distilled water, and finally a fragment be torn away from the olfactory region, we shall see distinctly how the epithelial cells split up into distinct cell groups (fig. 339). In these groups we distinguish an external half, composed apparently of extremely fine fibrils, which at their outer extremities terminate in long fine cilia, and an internal half, composed of large closely compressed nuclei, of which one is larger than the remainder, presents an elongated oval form, and is for the most part situated externally. Further manipulation with needles shows that each of the above-described groups consists of two kinds of cells, some few of which are large, whilst the greater number have a large round nucleus and very long fine processes (fig. 340). One of these processes, and indeed the thicker of the two, runs outwards, the other is very fine, is directed inwards, and can be followed to the margin of the subepithelial connective tissue. These are the olfactory cells of Max Schultze which conduct the impressions of smell. Their outer extremity bears the above-named long and fine cilia,* and appears in preparations which have been macerated in Müller's fluid sinuously curved, and as it were in zigzags. In specimens prepared with chloride of gold, or in those which have been treated with sulphuric acid, these processes present the appearance of very fine and varicose fibres. By the use of high powers it may be demonstrated that a continuous fine fibre runs through all the

* The apparent difference of the above from Max Schultze's observations, according to whom the cilia are absent in the Proteus, and as in branchiated animals, must necessarily be absent, can only arise from the circumstance that this most careful inquirer had only animals at his command that had long been preserved in solution of chromic acid.

enlargements, and from thence we may conclude that the external process of the olfactory cells is composed of twó substances throughout its whole length, an external, which swells up under the influence of certain reagents, and an internal thread which remains unaffected. The central process of the olfactory cells presents the same relations, with this difference only, that it is considerably finer, and in many instances is immeasurable. In Tritons I have found that the length of these processes, taken together with the other portions of the olfactory cells, sometimes exceeds by many times

Fig. 341.

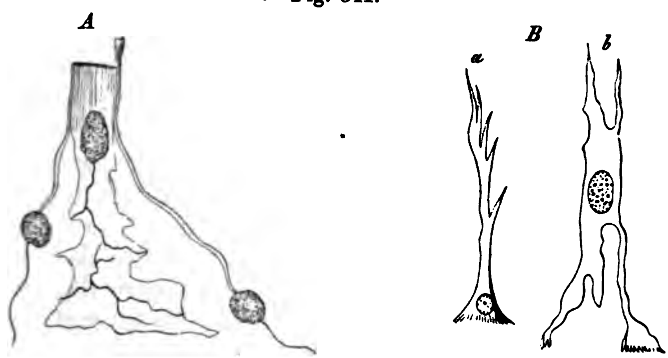

Fig. 341. *A*, an epithelial and two olfactory cells from the point of transition of the olfactory region into the ordinary mucous membrane (from the Triton); *B*, peculiar epithelial cells faom the olfactory mucous membrane; *a*, from the Raja clavata, after Max Schultze; *b*, from the Proteus.

the thickness of the epithelial layer (fig. 341). They must consequently either penetrate into the subepithelial layer, or run in a horizontal direction along the line of demarcation between it and the epithelial layer. I have actually observed the latter course in the Proteus. The cells that have just been described everywhere surround the above-mentioned large cells that possess a large oval nucleus, and extend through the whole thickness of the epithelial layer; their external half appears to be more or less cylindrical in the Triton and Proteus, is transparent, and often distinctly striated longitudinally (fig. 340). I have been able to satisfy myself that this striation is not to

be regarded as the optical expression of the surrounding olfactory cells. Moreover, it does not affect the whole thickness of the cell, but is limited to the surface. At the external extremities of the cells, which are free from cilia, a row of minute points can be distinguished, which encircle the entire extremity, and do not call to mind the appearances presented by the ordinary columnar epithelial cells at the surface. The inner half of the cells in question are not so uniform as the external, yet I very much doubt the statements made by several authors, that they consist of branching processes. They exhibit a great variety of forms, and we may represent these halves as more or less thick cylinders, composed of a soft and transparent mass, in which the round bodies and granules of the olfactory cells are everywhere imbedded. Folds thus originate, the borders of which, sharper than the remaining substance, project, giving rise to the appearance of figures that simulate the processes of authors. But by staining with anilin it may be shown that a very delicate transparent and longitudinally striated substance is stretched between these processes. The independency of this striation comes still more clearly into view at the base, where it altogether fails to give the impression of the presence of fibrous elements. The internal process gradually enlarges in a cone-like manner towards the subjacent connective tissue, and breaks up into numerous very short fibrils. It is very remarkable that the internal process presents a different appearance under the influence of many reagents. If for example the epithelial cells of the Proteus be treated with Müller's fluid or with iodized serum, and be then placed for a short time in diluted glycerine, all traces of the transparent substance vanish, and the above-mentioned folds make their appearance in the form of branched processes. If the mucous membrane of the olfactory region of an animal which does not exhibit any decided coloration of this part be treated with nitrate of potash, we obtain a very delicate picture, which shows distinctly how the olfactory cells are topographically related to those just described. Annular figures, which appear to be the ends of large cells, come into view, surrounded by a number of black dots, which are more or less closely arranged in different animals, and which are simply

the extremities of the olfactory cells (fig. 342). The relations just described are found to occur with very unimportant modifications in all animals, and even amongst the Invertebrata, as in the Cephalopoda (Sernoff).

Max Schultze, however, states that in Man, as well as in Mammals generally, the olfactory cells have no cilia, or, as he terms it, no olfactory hairs; in other words, he maintains that these hairs form no necessary condition for the perception of smell, and therefore are not deserving of any special name. When the olfactory hairs are present (as in Birds and Amphibia), they appear either in the form of stiff hairs, of which only one is supported by each cell, or of a bundle of fine cilia. In some few animals olfactory cells occur possessing both kinds of hairs. Occasionally that portion of the olfactory cell where the nucleus lies is fusiform. In some animals the external processes

Fig. 342.

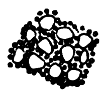

Fig. 342. Surface view of the epithelial layer of the olfactory region, after treatment with nitrate of silver. From the Proteus.

are remarkably thick, in others they are delicate, and become varicose under the influence of macerating fluids. Max Schultze has further demonstrated that the large epithelial cells are, in many Mammals, more or less strongly pigmented, the yellow pigment lying either near the outer surface or nearer their centre, and that to the presence of this pigment the above-mentioned tint of the olfactory region is due. Both in Man and Mammals generally, epithelium, free from olfactory hairs, occurs in this region; and although in the former ordinary ciliated epithelium occurs here and there, no true olfactory cells can be found interspersed amongst the others. In the Plagiostomata, on the contrary, the parts capable of perceiving odours are especially covered with ciliated epithelium.

Besides the two kinds of cells just described, another kind exists in the Plagiostomata (Max Schultze), in the Proteus and Triton (Babuchin), and perhaps also in many other animals,

which are likewise intercalated in the epithelial layer, and which call to mind the forked cells of Engelmann. Their form is very various, and is represented in fig. 340, *B*. They are in immediate contact, by their central extremity, with the subepithelial layer, and here frequently break up into very fine short fibrils. Their peripheric extremity does not reach to the surface of the epithelial layer, and is either conically pointed or branched. Their form, moreover, as above mentioned, is very variable, so that in the Proteus, for example, we meet with cells that, owing to their ramification, are very similar to the multipolar nerve-cells.

Lastly, it is not uncommon in young animals, and in the deeper part of the epithelial layer, to meet with round cells, destitute of any processes, which we may no doubt regard as destined to develop into the olfactory and epithelial cells.

The conducting apparatus of the olfactory organ is composed of the so-called olfactory nerves, which, as is well known, arise from the two bulbi olfactorii, and, according to the animal, either constitute a single nerve trunk, or form several strands, and then ramify in the mucous membrane of the olfactory region. The trunks of the olfactory nerve, which may be very readily broken up into fasciculi, run either horizontally or obliquely, in the glandular layer. From these trunks numerous branches are given off, which, undergoing further subdivision at different angles, run outward to the epithelial layer, and in specimens prepared with chloride of gold may be distinctly followed to its deep surface. On the other side the branches of the nerves run to the base of Bowman's glands.

The minute anatomy of these nerves has been sufficiently examined by Max Schultze, and has been already discussed at pp. 162, *et seq.*, of the first volume of this work. I am unable, however, to agree with the statement of this observer, that the olfactory nerves contain primitive nerve fibres, which are constructed on the type of those of Remak, that is to say, of a nucleated sheath of Schwann and fibrillar contents. Max Schultze states that the funiculi of the olfactory nerves split up into fasciculi of primitive fibres, and that in some few animals these fasciculi consist of fibrils, and are enclosed in a nucleated sheath, which he names the sheath of Schwann;

whilst in others the fasciculi of primitive fibres split into primitive fibres within their sheath, and these again are composed of fibrils and a sheath of Schwann. So far as my observation has extended, however, the fasciculi in question, whether they are provided with a sheath or not, consist in all animals of extremely fine fibrils kept in position by a finely granular mass. In some animals nuclei are sometimes seen in addition, disposed in regular rows between the fibrils, in consequence of which the whole fasciculus is divisible into secondary fasciculi destitute of a sheath. The sheath of the primitive fasciculi cannot represent the sheath of Schwann, but is rather to be compared, from a morphological point of view, with the neurilemma, with which also its peculiarities and structure may perhaps agree. We may also reasonably admit this even where the fibrils contain no nuclei between them, or form no secondary fasciculi, as occurs for example, according to Max Schultze, in the Pike. If in this case we were to regard the sheath as Schwann's sheath, we must do so also when the fibrils split into secondary fasciculi within the sheath, which fasciculi, according to Max Schultze, are again provided with a Schwann's sheath; we should be obliged to admit, in other words, that the nerve fibres possessing a nerve sheath, are again enclosed in a common sheath of Schwann. I may also remark in addition that I was unable to satisfy myself that the primitive-fibre fasciculi in many animals, especially in Plagiostomata, possess any sheath at all. The history of the development of the peripheric nervous system suggests that the olfactory nerves are to be regarded as embryonal structures that remain persistent at the second grade of their development, whilst the fibres of Remak attain the ultimate stage. The nuclei found between the fibrils of the olfactory nerves are, for the most part, true cells. They are not unfrequently fusiform, and in this case adhere, by means of their fine processes, very firmly to the nerve fibrils. I shall have an opportunity of entering into fuller details respecting them in another part of this work.

The question that now arises is, what becomes of the nerve fibrils when they have reached the epithelial layer? Unfortunately it can only be answered hypothetically. Examinations instituted on specimens stained with chloride of gold by no

means prove that the nerve fibrils end in the same mode as has been observed in the transparent cornea, though this might, indeed, be presupposed. After my discovery, that the large epithelial cells present throughout their whole length delicate longitudinal striæ, which, however, are only visible under favourable circumstances, may we not presume that the finest fibrils of the olfactory nerves, after they have penetrated the epithelial layer, everywhere closely embrace the large epithelial cells, and thus reach the surface of the epithelium? This presumption gains in strength, if we take into consideration that the conical internal extremities of the large epithelial cells break up into short delicate fibrils. I believe, however, that such a statement would at the present time be a little premature; for the number of instances of striated cells recorded increases daily. Thus, for example, it has long been known that the fibres of the lens are frequently longitudinally striated. Pflüger has observed striation in nearly all the cells composing the salivary cells. I have myself seen that a regularly disposed striation may be produced by the action of certain reagents on the crystalline lenses of some Crabs. Lastly, I have observed that even the contents of the cup cells sometimes appear to consist of very fine fibrils. This admonishes us to regard the striæ with considerable caution, and not to consider everything that is striated to be a nervous structure. I must also call attention to the fact that in the Triton, at the point where the epithelium of the olfactory region passes into the ordinary epithelium, where both the olfactory and epithelial cells become shorter and thicker, the internal extremities of the epithelial cells are enormously broad, and yet exhibit no indication of striæ (fig 340).

Max Schultze long ago advanced the hypothesis that the fibrils of the olfactory nerves enter into connection with the inner extremities of the olfactory cells. As essentially supporting this hypothesis, he referred to the very complete analogy which obtains, both in a chemical and in a morphological point of view, between the central extremities of the cells in question and the nerve fibrils. As additional evidence in favour of this hypothesis, I may add that under the influence of chloride of gold the olfactory nerves constantly assume a blackish violet colour, and although very rarely, still in suc-

cessfully coloured specimens the processes of the olfactory cells also become distinctly stained, whilst the nucleus remains pale and transparent. I possess a preparation made from a tortoise, unique amongst many hundred sections, in which the direct passage of the nerve fibrils into the epithelial layer is observable. In this instance branches arise from the deeper-lying trunks of the olfactory nerves, and run nearly vertically towards the epithelial layer. These branches are fibrillated, and are beset with nuclei subdividing as they continue their course to the attached surface of the epithelium; they here break up into fibrils and extremely fine fasciculi, which spread out horizontally for a very short distance, like a fan, and then run perpendicularly, but in an irregularly sinuous manner, into the epithelial layer itself, where they may be followed as far as to the nuclei of the olfactory cells. M. Schultze's hypothesis would become matter of fact if in the chloride of gold we possessed an agent that stained nervous elements alone, and was less capricious in its action, so as to produce no illusory appearances. We find also, as mentioned above, in the epithelial layer of the olfactory region, the peculiar cells which very closely resemble the forked cells of Engelmann. Whether we should regard these as constituting the terminations of the nerves is questionable.

In many instances appearances are presented which render it quite evident how the secondary fibrils, united into fasciculi, penetrate into the epithelial layer, and run for a considerable distance outwards between the epithelial cells, which is obviously suggestive of their terminating with free extremities (fig. 338, *C*). This is in apparent contradiction to what has been said in our earlier statements respecting the termination of the nerves, but the opposition is only apparent. If we admit that, as I have satisfied myself with the adoption of every precaution, the olfactory region is sensitive, if we further consider it to be highly probable that sensibility and smell are communicated by separate nerves, it immediately suggests itself to consider the free nerve ends I have observed as belonging to the fibres of simple sensation. Max Schultze has moreover already observed medullated between the non-medullated fibres.

The question in regard to the relation of the olfactory fibrils

to the central part of the olfactory organ is not less difficult to answer. It has long been known, through the researches of Walter (6), Leydig (7), Max Schultze (4), and has recently been confirmed by Meynert (8), that the fibrils of the olfactory nerve arise by fasciculi from the large spherical bodies which are imbedded in the bulbus olfactorius. Still, as Kölliker states in his work, the minute anatomy of these structures has not been thoroughly investigated. The best results are obtained by the investigation of their various relations in Plagiostomata, where they possess the same constituent parts as in the central apparatus of higher animals, though isolated and far apart from each other. In the Torpedo, for example, the bulbus olfactorius lies immediately upon the olfactory fossa, and is united by means of the long and slender tractus olfactorius with the olfactory lobes (?) (Scheinlappen), whilst the sheath of the tractus is continuous with that of the bulbus, in which the above-named spheroidal structures are distributed without any definite arrangement. They are separated from one another by nerve fibres and vessels, appear in the form of a finely granular structure, and are apparently beset externally with nuclei. In the Torpedo it may easily be demonstrated that these apparent nuclei are unquestionably very small cells, some of which are bipolar, whilst the majority are multipolar. One of the processes of these cells is sometimes smooth, and runs towards the tractus olfactorius, where it becomes invested with medullary substance. The other processes are at first thick, but subsequently divide into an infinite number of branches, which penetrate the spherical corpuscles. In the bipolar nerve cells the more delicate process passes into the tractus olfactorius; but the other, which is of distinctly fibrillar structure, penetrates into a spherical body, where it breaks up into extremely fine fibrils. The fibrils in some instances enter divergingly into a spherical body, without any definite arrangement, and emerge again from one side, united into a fasciculus; in other instances they already unite in the spherical body itself into a fasciculus which forms a kind of spire or coil, and then associates itself with the other fasciculi of the olfactory nerves (fig. 343).

What morphological significance are we to attribute to the

spherical bodies in question? Are they special and peculiar structures, or do they find their analogues in the nervous system? Although at first sight they appear to be finely granular, extremely thin sections present precisely the same appearance as the so-called molecular layer of the retina. It would not however, it appears to me, be quite correct to admit that we have here a reticular or spongy tissue before us. It is rather a convolute of extremely fine fibrils, the origin of which we are already acquainted with, and between which is a considerable quantity of finely granular substance. Similar relations are met with wherever there are only naked nerve

Fig. 343.

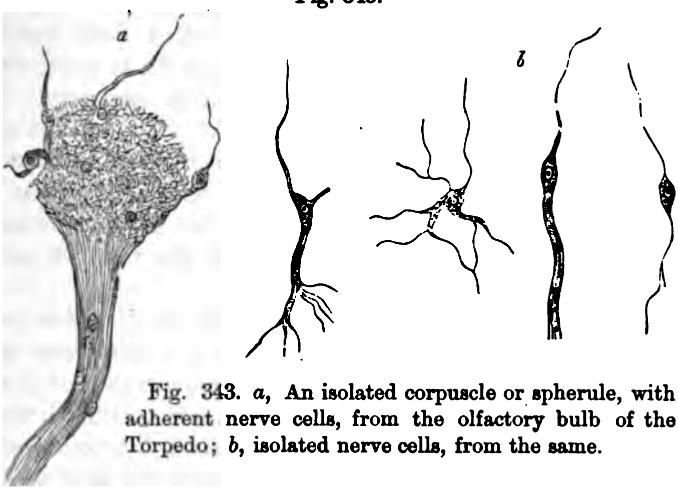

Fig. 343. *a*, An isolated corpuscle or spherule, with adherent nerve cells, from the olfactory bulb of the Torpedo; *b*, isolated nerve cells, from the same.

fibrils, or it may be the finest axis-cylinders, or in other words, where the nerves have not reached the higher grades of development. When such fibrils run parallel to each other, as is the case in embryonal and in the olfactory nerves, the fasciculi of fibrils offer a striated granular aspect. The smallest granules, or perhaps a substance which only changes into granules under the influence of certain reagents, cleaves so strongly to the fibrils, and glues them so firmly together as to render their isolation very difficult. But when the fibrils assume an irregularly convoluted course, we obtain the appearance presented by the reticular connective tissue, which is

chiefly occasioned by the granules; and the isolation of the several nerve fibrils then becomes almost an impossibility, as we find to be the case in the spherules of the regio olfactoria. I am very much inclined to believe that the same relations are repeated in the retina, and perhaps in other parts of the nervous system.

The tractus olfactorius consists exclusively of medullated nerve fibres, which have no sheath of Schwann. After they have reached one of the two projections, which in the Torpedo are placed at the sides of the great hemispheres, they penetrate into the reticular substance, gradually lose their medullary layer, and unite there with numerous small nerve cells, of which some again are bipolar, whilst others are multipolar. This is the essential fact I have discovered from my researches upon the Plagiostomata. I am unable to pursue the examination of the other constituents of this apparatus. All the relations just described respecting the origin of the nervus olfactorius are present also in the higher Vertebrata, however different their structure may at first sight appear to be. The fibres of the olfactory tract arise directly from a finely granular reticular mass, whether in the form of spherules or otherwise.

This mass is everywhere surrounded by small nerve cells. The processes which run inwards into the olfactorius and the cerebrum everywhere undergo conversion into medullated nerve fibres, which here and there unite again with fresh nerve cells. A difference consequently only exists in a topographical point of view, which must obviously be regarded as of merely secondary importance, and belongs to another chapter of this work.

[During the final revision of these sheets Exner has published in the *Wiener Sitzungsberichte* the results of his researches upon the olfactory mucous membrane of the Frog. According to what I can learn from his short provisional communication, the branches of the olfactory nerves break up into a plexus between the connective tissue of the mucous membrane and the epithelial layer, and from this the central processes both of the so-called olfactory cells and of the epithelial cells arise. The trigeminal fibres form a wide-meshed plexus in the connective tissue of the mucous membrane.—STRICKER.]

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CHAPTER XXXVI.

THE EYE.

The Retina.

By MAX SCHULTZE.

The retina is the membrane-like terminal expansion of the optic nerve lining the posterior part of the globe of the eye. In addition to nerve fibres, it contains various forms of nerve cells, which are intercalated in the course of these fibres before they reach their peripheric extremity. The extremity itself is characterized by a peculiar terminal apparatus, forming the layer of rods and cones, which are invested by pigment. The nerve fibres and nerve cells of the retina are imbedded in a spongy connective-tissue substance, which may be regarded as a continuation of that of the optic nerve, and presents great similarity to the connective tissue of the central organs of the nervous system. A part of this connective tissue is formed by bloodvessels, and probably also by lymphatics.

The textural elements of the retina are arranged in layers parallel to the surface of the spherical external membrane. The innermost of these, in immediate contact with the vitreous, is formed by the limiting layer of the spongy connective tissue which is often intimately connected with the surface of the vitreous, and is named the membrana limitans interna; its adhesion to the vitreous sometimes renders the detachment of the retina in the vicinity of the ora serrata, in fresh or well-preserved specimens, extraordinarily difficult. The most external of the layers is that of the rods and cones, including the pigment sheaths, which are formed by a special cell-layer—the pigment cell-layer of the retina. This rests upon the choroid, and, indeed, upon the vitreous connective substance of the chorio-capillaris, to which, on separation of the retina, it

often remains adherent, in which case the layer of rods and cones drawn out of their pigment sheaths constitutes the most external layer of the retina. A part, however, even of these not unfrequently remains behind with the pigment of the choroid,

Fig. 344.

Fig. 344. General view of the layers of the retina of Man. Magnified 400 diameters. The numbers refer to the explanation given in the text.

so that in well-preserved specimens we find the pigment sheaths do not easily permit the detachment of the enclosed portion of the rods, the latter adhering with the pigment to the choroid, whilst the inner portion of the rods cleaves to the retina.

The retina is composed of several layers, the synonyms of which threaten to perplex ophthalmological literature. It is therefore of importance to name the various layers in the simplest manner possible. The terms employed by Heinrich Müller in all his publications upon the retina have proved the most serviceable, and with a few modifications may still be retained. The only terms I have introduced are my membrana limitans externa and the division of the intergranule layer of H. Müller into two layers. I indeed first called attention to the necessity of making this division, and whilst preserving the name of intergranule layer to that constantly present layer of finely granulated substance which lies between the internal and external granules, have dissociated from it that portion of the external granule layer composed of the rod and cone fibres, which is particularly strongly developed at the yellow spot in Man, and which was included by Müller (1) in his intergranule layer. Henle calls the intergranule layer, as I define it, the external granulated layer, and thus expresses its similarity in structure with the molecular or internal granulated layer; the radially fibrillated division of the external granule layer, on the other hand, he terms the outer fibrous layer. In order to obviate misapprehension in the explanation of the name intergranule layer, which, it will be seen from the above, in consequence of H. Müller's publications, differs somewhat from mine, we shall hereafter term it Henle's external granulated layer instead of the "intergranule layer." In accordance with the nomenclature here employed, the layers of the retina from within outwards are as follows:—

1. Membrana limitans interna.
2. Optic-fibre layer.
3. Ganglion-cell layer.
4. Internal granulated (molecular) layer.
5. Internal granule layer.
6. External granulated (intergranule) layer.
7. External granule layer, including the external fibre layer, which is present in certain parts of the retina.
8. Membrana limitans externa.
9. Layer of rods and cones.
10. Pigment layer.

All the layers of the retina lying between the two limiting layers are composed of the two different elementary parts which have already been named *elements of the nerve tissue*, and *elements of the connective tissue*. This is admitted on all hands. The differences of opinion that exist relate to which of the two groups of tissues this or that fibre, this or that cell, belongs. This disagreement, as our researches on the mode of termination of the nerves at the periphery and in the centres show, depends on the extremely embarrassing circumstance that very fine non-medullated nerve fibres are indistinguishable by any absolutely certain characteristic, even where high powers are used, from other kinds of fibres, especially where both kinds are intimately interwoven with each other, as undoubtedly occurs in many parts of the retina. In order to obtain a starting-point to enable us to determine the distinction between these two kinds of fibres, we shall commence our consideration of the minute anatomy of the retina with that of the undoubted nerve fibres which spread out divergingly from the optic nerve, and form the layer of optic-nerve fibres immediately succeeding the membrana limitans interna. With the knowledge thus gained we shall proceed to investigate, and endeavour to distinguish, the nerve fibrès of other layers, which cannot be shown to be continuous with true nervous elements. We shall then describe the supporting connective tissue in a special section, as well as the modifications of structure presented by the retina at the macula lutea, the fovea centralis, and ora serrata. The vessels of the retina will be elsewhere described.

THE NERVOUS ELEMENTS OF THE RETINA.

The optic nerve, at the point where it reaches the external surface of the globe of the eye, consists, just as in its whole course through the orbit, (independently of its sheaths, bloodvessels, and lymphatics,) of medullated fibres, which are grouped into fasciculi, and are imbedded in relatively dense connective tissue. On breaking up small portions, we meet, when examined in the fresh condition, and in indifferent fluids, with short pieces of nerve fibres and with rounded and cylindrical masses of nerve

medulla, which resemble the elements of the white substance of the brain.* Longer portions of medullated nerve fibres may be isolated by teazing out fine longitudinal sections of the optic nerve preserved in hardening fluids. These also resemble the medullated fibres of the white substance of the brain, when subjected to similar treatment, in the circumstance of their surface being beset with knots and varicosities.† It would therefore appear that the fibres of the optic nerve resemble those of the brain in being destitute of the sheath of Schwann. The superior firmness of the optic nerves to the brain substance is sufficiently explained by the large amount of dense connecting substance they contain, the presence of which can be demonstrated in fine transverse sections of the hardened nerves. Each fasciculus of nerve fibres is separated from the adjoining ones by a thick layer of highly vascular fibrillar connective tissue.‡ Extremely instructive specimens may be obtained from sections of this kind, if taken from optic nerves which have been hardened for a short time in a strong solution of perosmic acid, or, as F. E. Schulze recommends, in chloride of palladium, or from fine sections otherwise hardened, coloured with chloride of gold (Leber), and explain how Klebs§ could maintain that the quantity of connective tissue in the optic nerves is often still more abundant than that depicted in fig. 5 of Plate xix. of the Icones physiologicæ. The differences existing between normal and atrophic optic nerves have been very exactly described elsewhere by Leber, so that at a rough guess the fasciculi of nerve fibres constitute about one half of the mass of the optic nerve. In every fasciculus,

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* This similarity of the fibres of the optic nerves with those of the brain, and their difference from other peripheric nerves, was first described and illustrated with many drawings by Ehrenberg, *Abhandlungen der Acad. der Wissenschaften zu Berlin aus dem Jahre*, 1854, p. 665, Taf. i.—v.

† See this Manual, p. 111, fig. 19.

‡ See the description and illustrations of transverse and longitudinal sections of these nerves given by Donders, in Gräfe's *Archiv*, Band i., Abtheil. 2, Taf. ii., figs. 2 and 3; by Henle, in his *Anatomie des Menschen, Eingeweidelehre*, p. 583; and by Leber, in Gräfe's *Archiv*, Band xiv.,—ii., Taf. v., fig. 1.

§ Virchow's *Archiv*, Band xix., p. 324.

nerve fibres of very various diameter are mingled together, the finer ones preponderating. As the nerve perforates the sclerotic at the so-called lamina cribrosa, all the nerve fibres, except in a few instances that will hereafter be mentioned, lose their medullary sheath. The diminution in the diameter of the nerve, thus occasioned, is rather sudden, and is accompanied also, according to Löwig,* by the internal connective tissue of the nerves becoming continuous with that of the sclerotic and choroid. What now remains of the nerve fibres is the extremely delicate axis-cylinder, completely deprived of its medullary sheath. These, enclosing the arteria and vena centralis, and always invested by a certain quantity of connective tissue, pass through the choroid, and as they radiate outward in all directions, bound the shallow crater of excavation of the optic disk† into the plane of the internal surface of the retina, where they form the optic-fibre layer situated immediately external to the membrana limitans interna, and the thickness of which gradually diminishes towards the ora serrata, so that at this latter line only isolated fibres or small fasciculi of fibres are demonstrable. At the yellow spot of the retina the layer of nerve fibres, considered as a continuous layer, suffers an interruption. The rest of the connective tissue of the optic nerve passes into the substance of the supporting fibres of the retina.‡

The nature of the nerve fibres forming the layer in question may best be examined under the microscope in the perfectly fresh state by placing portions of the retina taken from the still warm bulb in vitreous humour, with the internal surface looking upwards. Under these circumstances we may sometimes, in the vicinity of the ora serrata, where the optic-nerve fibres run separately, obtain very well-marked specimens, pro-

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* *Studien des Physiolog. Instituts zu Breslau, herausgegeben* von Reichert, 1858, p. 125.

† H. Müller treats of the so-called physiological excavation of the entrance of the optic nerve in Gräfe's *Archiv für Ophthalmologie*, Band iii., Abtheil. ii., p. 86. L. Mauthner refers in a more extended manner to the recent literature upon the subject in his *Lehrbuch der Ophthalmoscopie*, 1868, p. 252.

‡ Klebs, in Virchow's *Archiv*, Band xix., p. 321, Taf. vii.

vided the granular coagulation which occurs soon after death in most of the cellular elements of the retina has not occurred. The isolation of the soft fibres by needles can only be very imperfectly accomplished in the fresh condition and in indifferent fluids, but may be effected in retinæ macerated in hardening fluids, as, for example, after preservation for some time in iodine serum, and in dilute solutions of chromic acid and of bichromate of potash. The nerve fibres of the retina thus brought into view *vary considerably in diameter*, many being only just capable of measurement, and therefore under half a micromillimeter, whilst the thickest have a diameter of from three to five micromillimeters. None of them present any traces of attached or imbedded nuclei, and very slight traces of any isolable sheath, or of a differentiation into cortex and medulla. They appear in the form of pale, pliable, very soft fibres, in which no further structure is perceptible than some indication of fibrillation and here and there a cluster of fine granules. All exhibit a great tendency to the formation of fusiform varicosities. In fresh preparations examined *in situ*, such varicosities however are almost entirely absent, and their formation can be retarded by the application of iodine serum or addition of common salt to serum, but is accelerated by dilution of serum with water, and is therefore undoubtedly a phenomenon of imbibition. The number, size, and form of the varicosities exhibit many varieties, but the appearances are always quite different from those presented by the medullated fibres of the brain or spinal cord. In the latter the surface is beset with varicosities, and rendered knotty by the partial escape of the strongly refractile medulla. No trace of such escape is perceptible in the retinal fibres; but the fusiform varicosities they present, correspond to those observed in axis-cylinders from which the medullary sheath has been detached, as may be seen for example in the fibres of the auditory nerve.*

That a change occurs in the texture of the optic fibres in the places where varicosities develop, is demonstrated by the fact that the varicosities, especially of the thicker fibres, exhibit

* M. Schultze's *Observationes de retinæ structura penitiori*, 1859, fig. 1.

for the most part in their interior, a granular change of the fibre-substance, whilst the parts which have not become swollen by imbibition remain homogeneous, and permit the fibrillar structure to be more or less distinctly recognized. That phenomena of imbibition here play an important part is shown by the behaviour of the nerve fibres of the retina in solutions of chromic acid, which when sufficiently concentrated prevent the formation of varicosities, whilst when rendered more and more dilute the number and size of the varicosities progressively increase, till at length the fibre, beset with enlargements till

Fig. 345.

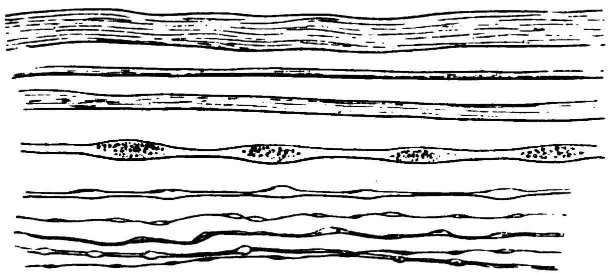

Fig. 345. Nerve fibres of the retina, with and without varicosities. *a*, From the Ox; the remainder from Man. Magnified 800 diameters.

it resembles a string of beads, altogether breaks up.* This occurs in the case of the finest fibres, the varicosities of which are relatively the largest from the very commencement, and are in more close proximity with one another, whilst they make their appearance earlier than in the thicker fibres.

Dichotomous divisions of the nerve fibres have been described and depicted by Corti† and Gerlach.‡ These occur as a rule in the optic-fibre layer, but are only exceptionally met with; the cases that have been described may possibly have been instances of the bifurcation of processes of ganglion cells.

* More precise statements in regard to the solutions in which varicosities occur, will be found in my Essay in the *Monatsberichten der Academie der Wissenschaften zu Berlin*, 1856, p. 511.

† Müller's *Archiv*, 1850, Taf. vi., fig. 3.

‡ *Handbuch der Gewebelehre*, 1854, p. 498.

The concordant statements of Michaelis, H. Müller, Henle, Kölliker, and others, show that at the yellow spot an interruption to the regular radiating course of the nerve fibres in the retina occurs, a continuous fibre layer being here defective, and the fibres losing themselves in the thick ganglion-cell layer, in order to enter into which freely, they form a series of arches in the vicinity of the yellow spot. Liebreich* has recently called attention to another peculiarity, namely, that many more nerve fibres proceed directly upwards and downwards from the point of entrance of the optic nerve, than outwards, though far larger tracks of the retina require to be innervated in the latter direction. The fibres accompanying the larger vessels, and running outwards, form arches around the macula lutea where they terminate.

On microscopic examination of an uninjured retina from the inner surface, the nerve fibres may frequently be seen to be grouped into fasciculi, between which are elongated fusiform spaces.† These are occupied by fasciculi of the radiating supporting fibres of the retina, which terminate in the membrana limitans interna. Where, as at the ora serrata, the nerve fibres are sparingly present; or as at the macula lutea, are altogether absent as a continuous layer, the ganglion cells come to be in immediate contact with the membrana limitans interna.

In exceptional cases in the human subject the medullary sheath of certain portions of the optic nerve is retained beyond the limits of the optic disk, and extends for some distance into the retina. This consequently is rendered opaque, and when examined by direct light appears white, as is well shown in the excellent ophthalmoscopic illustrations given by Liebreich in his Atlas of Ophthalmoscopy, Taf. xii., figs. 1 and 2. Virchow ‡ first established this fact in a man aged forty-six, in whose eyes, after death, he found medullated fibres around both disks, in one eye presenting the appearance of four diverging radii; in the other a hazy white annulus; and since that date a series of similar cases have been observed and examined both anatomically

* Zehender, *Klinische Monatsblätter für Augenheilkunde. Jahrgang*, vii., p. 457.

† See H. Müller and Kölliker, Retina-tafel in Eckers' "Icones," etc., fig. 14.

‡ Virchow's *Archiv*, Band x., p. 190.

and optbalmoscopically. Two varieties have been noticed, in one of which the medullated fibre tract is continuous with the optic disk,* whilst in the other and less common case isolated white spots appear upon the retina at some distance from the disk, so that here the medulla, after disappearing at the point of entrance of the optic nerve, reappears after the fibres have run for a certain distance.†

Amongst Mammals it has been known since the time of Bowman that medullated nerve fibres were prolonged into the retina in the Rabbit and Hare.‡ In these animals two white fasciculi run divergingly outwards in opposite directions, which render the retina moderately opaque, but perhaps are not altogether incapable of perceiving light, since, as I have satisfied myself, the bacillar layer is well developed behind them.

A small quantity of medullary substance, which however scarcely interferes with the transparency of the optic-fibre layer, is found, as Leydig has pointed out, around the nerve fibres of the retina in many Fishes, and he remarks that the primitive nerve fibres of Sharks and Rays are "sharply contoured and varicose.§ H. Müller also mentions the fact that some of the fibres within the globe of the eye in Fish are composed of axis-cylinder and medullary sheath.|| A somewhat similar appearance may also be seen in Birds.

A very remarkable deviation from the normal condition is exhibited in the thickenings of the nerve fibres of the retina, which in cases of Bright's disease were regarded as the cause of certain white spots occurring in this affection, and were considered to be bipolar ganglion cells. These varicosities resembling bipolar ganglion cells were first described by Zenker and Virchow, and their true nature was recognized by H. Müller.¶ They are formed of fusiform thickenings and

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* Donitz (Reichert and Du-Bois Reymond's *Archiv*, p. 741, 1864), by whom this persistence of medulla was first demonstrated ophthalmoscopically, established the fact that in his own eye the part in question was, like the disk itself, blind; *i.e.*, is either quite incapable of transmitting light, or that there is no layer of rods and cones behind it.

† See for example the cases given by v. Recklinghausen in Virchow's *Archiv*, Band xxx., p. 375.

‡ See H. Müller, *Zeitschrift für wissenschaftliche Zoologie*, Band viii., p. 64.

§ *Beiträge zur Mikroskop. Anat. und Entwicklungsgeschichte der Rochen und Haie*, p. 24, 1852.

|| *Zeitschrift für wissenschaftliche Zoologie*, Band viii., p. 22.

¶ v. Gräfe's *Archiv für Ophthalmologie*, Band iv., 2, p. 41.

condensations of the non-medullated fibres; their substance is firmer and more lustrous than the healthy axis-cylinder, and is capable of resisting decomposition for a longer period.

Section of the optic nerve in the orbit in animals is followed by atrophy of the nerve-fibre layer (Lehmann), and this, according to Krause, is preceded by a deposit of fat molecules in the transparent pale fibres, which form of degeneration extends to the elements of the following layer, to wit, the ganglion-cell layer.

On the outer side of the nerve-fibre layer, and extending over the greatest part of the retina, is a simple layer of nerve cells or corpuscles, separated by interspaces of various size, which is designated the *layer of ganglion cells.* Near the macula lutea of Man, two or three such cells are superimposed upon one another, whilst at the yellow spot itself, with suppression of the nerve-fibre layer, the ganglion cells come to be arranged in a single layer. The size of these cells varies to an extraordinary extent in the same retina; so that small ones not exceeding fifteen micromillimeters are found in close proximity with others of double that size or more. All have the peculiar finely granular appearance of the cell substance presented by the nerve corpuscles of the ganglia of the central organs, and are for the most part without yellow pigment,* which it is well known often occurs in other nerve cells; they contain a relatively large homogeneous transparent nucleus, with the large nucleoli that all ganglion cells possess, and in the interior of this again, is here and there a small vesicle or granule. Notwithstanding the difficulty of isolating perfect specimens of these cells, a large number of observations have been made on the long and branched processes, which, like the ganglion cells of the nervous centres, they give off. A particular condition of maceration of the retina, not easily hit upon, appears to be requisite in order to permit the isolation of these cells to be satisfactorily accomplished; at least, we can only thus explain the circumstance that the best preserved processes of these cells that have hitherto been observed, were obtained

* According to Corti, the ganglion cells of the retina of the Elephant have a yellowish or yellowish-brown colour.

from the eyes of an Elephant, that were not removed from the body until seven days after death.*

Ganglion cells, with their processes, may be observed in the perfectly fresh retina, if portions taken from the neighbourhood of the ora serrata, and from the surface of which the vitreous has been removed, are examined in serum, with this surface upwards. Lying among the decussating nerve fibres, and immediately beneath the membrana limitans interna, in the same plane with the capillary bloodvessels, numerous ganglion cells may be then seen, which, by cautious manipulation, the production of a cloudy appearance by coagulation being avoided, and the pressure of the covering glass being gradually increased, become more and more distinct, and well adapted for observation, even with the highest powers. Such, so to say, living ganglion cells (fig. 346, *A*) present an extraordinary degree of transparency, since they contain only very small granules in their cell substance, and are composed essentially of an almost hyaline mass, in which the perfectly transparent nucleus, with its lustrous and often finely dentated nucleoli, lies imbedded. Dead ganglion cells which in such preparations may be found at the margin of the section, or where the retina has been otherwise injured, present a totally different aspect, becoming, by coagulation, coarsely granular and perfectly opaque. More minute examination of the former with higher powers, shows that the fine granules of the cell substance lie to some extent in rows, and are grouped in parallel striæ, whilst the non-granular cell substance appears also differentiated into bands. This character is precisely similar to that which I first described as occurring in the ganglion cells of the brain and spinal cord.† The cell substance is hence probably fibrillar, and contains, in addition, an interfibrillar granular substance; but the transparency of the cells of the retina during life is so great, and the fibrils are so fine, that the image they present is less distinct than that, for instance, of the cells of the spinal cord. In the next place, the fibrils around the nucleus possess an approximatively concentric arrangement, whilst at the peri-

* Corti, *Zeitschrift für wiss. Zoologie*, Band v., p. 90, Taf. v., 1854.

† In this Manual, Vol. i., p. 171 *et seq.*

phery they pass into the processes springing from the ganglion cells. Several such processes may often be seen in fresh preparations, of considerable thickness, and undergoing more or less ramification. If a process runs out unbranched and straight, it cannot, either by its refractile power or its intimate structure, be distinguished from the fibres of the optic nerve, since the latter, as has been mentioned above, likewise possess a fibrillar structure. This extremely delicate fibrous structure of

Fig. 346.

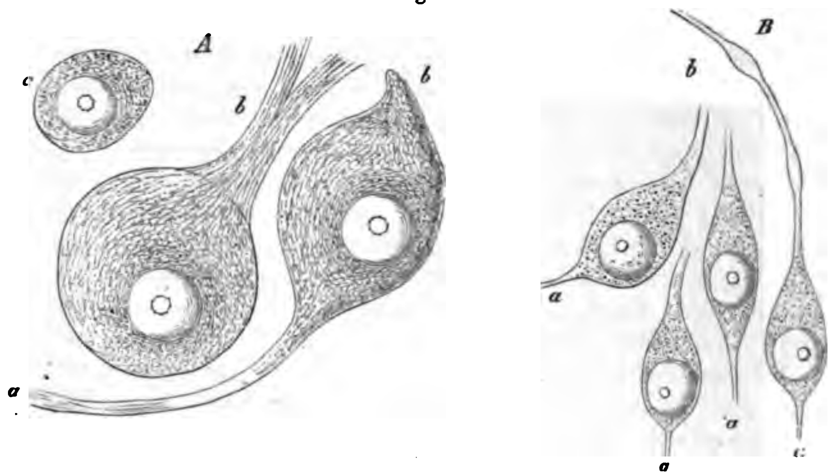

Fig. 346. *A*, Ganglion cells from the fresh retina of the Ox, taken from the neighbourhood of the ora serrata, *in situ*; *a*, nerve-fibre process passing into a fasciculus of optic fibres; *b b*, processes which lose themselves in the granulated layer; *c*, small ganglion cells, very commonly found near the larger ones. *B*, Ganglion cells of the macula lutea of Man; *a*, their central; *b*, their peripheric process. Magnified 500 diameters.

the ganglion-cell substance cannot be rendered more distinct by the aid of reagents; but, on the contrary, it rather tends to disappear with the occurrence of granular coagulation. Even iodized serum and perosmic acid destroy the transparency of the cells.

Surface views of still living retinæ are obviously not well adapted to enable a correct estimate to be formed of the *number of processes* given off by the ganglion cells. In many

of the cells it is scarcely possible to see whether any processes are given off at all, either on account of their being so closely compressed against one another, or because they are covered by the fibres of the optic layer. The results of the examination of teazed-out preparations and sections, so far as they have been at present used for the study of the ganglion cells, show that the number of these processes, like those of the ganglion cells of the central organs of the nervous system, varies considerably. Cells with many processes have been most commonly depicted, but many cells also occur with only two processes, as at the yellow spot (fig. 346, *B*), and unipolar cells have also been described.

In 1850, Corti* pointed out the similarity of the appearance of some of the ganglion-cell processes to fibres of the optic nerve layer, and, relying essentially upon the above-described fusiform varicosities, which occur in both, came to the conclusion that the optic-nerve fibres were directly continuous with the ganglion cells. Attention has been called to the agreement in character of the ganglion-cell processes with the nerve fibres of the retina, by Remak, Hannover, H. Müller, Kölliker, and many others. The cells lie in immediate contact with the layer of nerve fibres, and are, in fact, interposed between the fasciculi of the latter, whilst their processes may be followed for considerable distances, and agree in all points with the fibres of the optic-nerve layer; under these circumstances it is impossible to doubt that the fibres are directly continuous with the cells. Another question is, whether all optic-nerve fibres are connected with ganglion cells *before they reach the external layers of the retina*. It is possible that a part of those differences in the function of the several optic-nerve fibres which we are compelled to admit on physiological grounds, stand in direct relation to the presence or absence of a connection between the fibres and the ganglion cells. Upon this point, however, no positive statement can at present be made.

According to a method suggested by Manz,† the optic layer

* Müller's *Archiv*, 1850, p. 273, Taf. vi.
† *Zeitschrift für rationelle Medizin*, Band xxviii., p. 231, 1866.

of the retina of the Frog can be so detached in specimens prepared with alcohol, that the ganglion cells come away with them,* and the connection of the latter with the optic fibres can thus be most distinctly brought into view. The majority of the cells then appear to be unipolar. Manz nevertheless admits that the numerous and probably peripherically directed processes of these cells, demonstrable by other methods, are broken off in this mode of preparation. We only know, therefore, in respect to these processes of the ganglion cells of the retina which do not disappear in the optic-fibre layer, that a portion run towards the granulated layer. Anastomoses of the cells with each other, effected by thick processes, have been depicted by Corti in the Elephant. It remains to be shown whether such connecting processes, which have not been again observed, are to be regarded as normal.

As in the optic-fibre layer, so also between the ganglion cells, the radiating supporting fibres form a kind of framework, which will be subsequently described.

Section of the optic nerve in animals is followed, according to W. Krause, by fatty degeneration of the ganglion cells.† In the eyes of blind persons in whom the disappearance of the layer of nerve fibres of the optic nerve can be anatomically demonstrated, there is usually also atrophy or complete absence of the ganglion cells, as is seen especially in glaucoma resulting from an increase of the intra-ocular pressure.

The peculiar appearance of the *internal granulated* (molecular) *layer of the retina* is due to the admixture of a very fine plexus of spongy connective tissue, given off from the hereafter-to-be-described radial supporting fibres, with immeasurably minute nerve fibrils. The latter, as Pacini ‡ and Remak § first pointed out, form an essential constituent of this layer. They may be isolated in properly macerated retinæ

* H. Müller (*Zeitschrift für wiss. Zool.*, Band viii., p. 21), even at that date (1856), remarked in regard to the retina of Fishes, that "if the nervous fibre layer were raised from the inner surface of the retina with forceps, a portion of the cells was easily detached with them."

† *Membrana fenestrata*, p. 38.

‡ *Nuove ricerche sulla tessitura intima della retina.* Bologna, 1844.

§ *Medicinische Centralzeitung*, 1854. No. 1.

for short distances, when they appear as extremely delicate and very tortuous fibres, beset with distinct fusiform varicosities, but otherwise smooth. The thicker and branched ganglion-cell processes which dip into this layer, or belong to it from their first origin from the cells, can be still more distinctly followed, though little is known in respect to their mode of termination. Some are continuous with immeasurably fine fibrils, which, after a circuitous path, at length reach the outer layers of the retina, whilst others, especially at the yellow spot, enter the inner granule layer in the form of thick fibres. Such statements have been made, amongst others, by H. Müller * and Kölliker,† Gerlach,‡ Manz,§ and Merkel.‖ The macula lutea, on account of its less resistant connective tissue, appears to be the part of the human retina best adapted to follow to their termination the nerve fibres running in the granulated layer. But inasmuch as the ganglion cells are here almost all bipolar, whilst they are elsewhere multipolar, it becomes a question whether great differences do not also exist in regard to the course pursued by these processes. Speaking generally, the same differences of opinion are held respecting the nature of this granulated layer as of the grey granulated substance of the cortex of the cerebrum.¶ In particular, it is doubtful whether, besides the fine and the very finest nerve fibres and the plexuses of the connective substance, a certain number of minute granules of unknown nature are not also present, as appears to be the case, or whether the nerve fibrils and spongy connective substance give rise by their peculiar disposition to the finely granular appearance.

In regard to the course and ultimate destiny of the processes of the ganglion cells and the fine nerve fibres of this layer, we must admit the impossibility of giving any positive statement

* *Zeitschrift für wiss. Zoologie*, Band viii., p. 61.

† *Icones Physiologicæ*, Taf. xix., fig. 12. λ.

‡ *Gewebelehre*, 2nd edition, p. 498, fig. 220.

§ *Zeitschrift für rationelle Medizin*, Band xxviii., p. 237.

‖ *Macula lutea*, p. 11, fig. 9.

¶ See inter alios H. Müller, *Zeits. für wissenschaft. Zoologie*, Band viii., p. 115; and Henle and Merkel, *Zeitschrift für rat. Med.*, Band xxxiv. p. 49, 1869.

on the basis of the preceding observations, and with the exception of those at the yellow spot. The internal granulated layer interrupts our knowledge of the course of the nerve fibres, which again become visible in the outer layers of the retina. The thickness of the internal granulated layer in Man varies, according to H. Müller, between 0·03 and 0·04 of a millimeter.

The cause of the appearance, in sections of the retina of many animals, of dark striæ, which run parallel to the surface, and give indications of a lamination of the granulated substance concentric with the tunics of the eye, has not as yet been satisfactorily ascertained. G. Wagner* states that he has counted eight such layers. The spongy connective tissue, as my investigations on the retinæ of Sharks show, takes some share in its formation, the meshes being somewhat smaller in the darker bands.†

The layer of internal granules which succeeds externally to the granulated layer contains, as Vintschgau‡ and H. Müller were already aware, two distinct kinds of cellular elements which are connected with two different kinds of fibres that pursue an essentially radial course. Besides the radial supporting fibres, which occupy a considerable space in this layer, and intercommunicate by numerous bridges and intercalated plexuses, there are numerous similarly radiating nerve fibres, the course of which only in some few instances differs from that of the supporting fibres, in being directed obliquely towards the surface of the retina.§ These exactly resemble the fibres of the optic layer, and are distinguished by their fusiform varicosities and smooth surface from the rough finely dentated supporting fibres. In both kinds of fibres nucleated spots are imbedded, and these represent the so-called internal granules.

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* *Sitzungsberichte der Marburger naturforsch. Gesellschaft*, Juli, 1868, No. 5, p. 47.

† *De retinæ structura penitiori*, fig. 5.

‡ *Ricerche sulla structura microgr. della retina dell' uomo, degli animali vertebrati e di Cephalopodi. Sitzungsberichte der Wiener Acad. d. Wissenschaften*, Band xi., 1853, figs. 1, 5, 6, 9.

§ In Falco buteo. Max Schultze, *Archiv für Microscopische Anatomie*, Band ii., p. 262. And, according to Hulke, in the yellow spot of Man, *Philosoph. Transact.*, 1868, p. 112.

Those of the supporting fibres, which are far less numerous than the others, will be subsequently described; whilst those which are introduced in the course of the nervous radial fibres, and which, in consequence of the large number of these last, are arranged in several superimposed layers, resemble small bipolar ganglion cells. But the quantity of their very finely granulated substance is small, and the nucleus is therefore relatively larger than in the case of the true ganglion cells; the nucleolus is very apparent in the homogeneous nucleus, but is again rela-

Fig. 347.

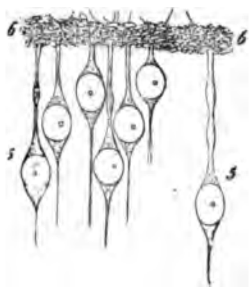

Fig. 347. Internal granules of the retina of Man. Magnified 800 diameters.

tively smaller than in the true ganglion cells. Of the two processes possessed by the inner granules, and which represent the nervous radial fibres, those that are periphericaly directed, as described by Merkel,* from the vicinity of the macula lutea, are usually thicker than the central one. In animals also the inner granules appear to have usually two processes,† though it is only by a happy accident they can be clearly isolated, and we are therefore still far from having an exact knowledge of the nervous inner granules and their processes in various regions of the retina, either of Man or of animals. A few inquirers, as Ritter,‡ have described more than two processes. Great variations occur amongst the inner granules. H. Müller states that in

* *Loc. cit.*, p. 11.
† M. Schultze, *Archiv. für Mik. Anat.*, Taf. xiv., fig. 9*b*, from the Cat. Hasse, *loc. cit.*, p. 257.
‡ *Wallfischauge*, p. 37.

Man, as amongst the Vertebrata generally, the innermost layer frequently contains somewhat larger granules. Besides these two forms and the nuclei of the supporting fibres, W. Krause* distinguishes a fourth kind of internal granules, which form the outermost layer, and project into the external granulated layer (Krause's membrana fenestrata). These he believes are unipolar, and have no connection with the outer layers of the retina,† but form the terminal organs of the optic fibres.

A structural difference exists in some animals, especially amongst Fishes, in regard to the cells projecting into the inner granule layer, which unite with the layer I have termed the fenestrated intergranule layer (stratum intergranulosum fenestratum).‡ I consider these to be formed by a special development of the connective tissue of the next layer.

The thickness of the internal granule layer in Man amounts, according to H. Müller, to 0·03 or 0·04 of a millimeter, diminishing towards the ora serrata, where, at most, three tiers of granules lie superimposed upon one another, to 0·02 of a millimeter, but increasing at the yellow spot to about 0·06 of a millimeter.

The layer of internal granules is separated from *the layer of external granules by an intergranule layer*, which consists of a thin layer of fine plexiform tissue enclosing a few nuclei and smooth cells, with coarser fibres running parallel to the surface of the retina, which are capable of being raised in the form of thin laminæ. In Man and the higher Vertebrata this appears in sections of the retina as a finely punctated granular layer, which, though much thinner, presents a very close resemblance to the internal granulated layer. On this account Henle designated it the *external granulated layer*, a term that, as already stated (p. 220), we shall adopt in order to avoid confusion with H. Müller's intergranule layer. W. Krause has recently employed the term membrana fenestrata to indicate it.

The external granule layer, in its simplest form, as seen in Man and Mammals, consists of a thin layer of granulated

* *Membrana fenestrata*, p. 42.

† See W. Krause's *Schema*, *loc. cit.*, Taf. ii., fig. 21, *gri*.

‡ *De Retinæ structura*, 1859, p. 13.

substance of tolerably equable thickness in Man, amounting to about ten micro-mill. through the whole retina. In the finely striated matrix of the connective tissue, extraordinarily fine fibrils are imbedded, which run without branching for considerable distances, either obliquely or parallel to the surface of the retina, and are to be regarded, like the similar ones of the internal granule layer, as nerve fibres, on account of the fine fusiform varicosities they present, and their otherwise smooth surfaces. These fibres are in part developed from the peripheric processes of the internal granules, and in part from the fibres of the rods and cones. Isolated nuclei are scattered generally in this layer, but probably all belong to the connective tissue, which at this spot presents many modifications in different animals that will be hereafter described. We possess no more information of the nervous fibres of this layer than of those of the internal granule layer. Their course deviates from the radial; and although, in occasional instances, fibres may be seen passing straight through it,* the greater number appear to form a fine plexus in the plane of the retina, so fine and complex, indeed, as to be equalled only by the grey substance of the central organs.

The rod and cone fibres, which form an essential constituent of the external granule layer, are rooted by their inner ends in the external granulated layer. All the so-called external granules are nucleated swellings of these fibres. The layer of the rods and cones is immediately superimposed upon the external granules, owing to the above-named fibres being in direct continuity with the latter. A sharp contour-line which in transverse sections of the retina divides the external granules from the rods and cones, constitutes the external limiting membrane.

In most parts of the retina of Man, and almost everywhere in animals, the space intervening between the limitans externa and the external granulated layer is not larger than is necessary for the disposition of the external granules (a single nucleus corresponding to each rod and cone) and the fibres belonging to them, putting aside the small quantity of connective tissue which

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* Hasse, *Zeitschrift für rat. Medicin,* Band xxix., p. 255.

is present in this layer. In this case, which is by far the most common, the external granulated layer forms a true intergranular layer. In the posterior part of the fundus of the eye, and sometimes in the vicinity of the macula lutea of Man, the space intervening between the limitans externa and the external granulated layer becomes much more considerable. Instead,

Fig. 348.

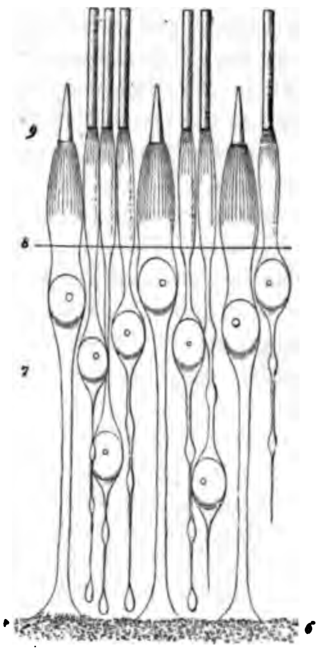

Fig. 348. From the posterior part of the fundus of the human retina. 6, External granulated layer; 7, external granule layer; 8, limitans externa; 9, rods and cones, the external segments of which are sharply differentiated from the internal cylinders. Magnified 800 diameters. The supporting fibres of the connective tissue are omitted in this figure.

however, of the external granules separating from one another, they remain in close apposition to the limitans externa, forming a multiple layer, whilst internally a free space appears, in which are no granules, and which is essentially occupied by the fibres of the rods and cones running to the external granu-

lated layer. If the whole space between the limitans externa and the external granulated layer is to be named the "external granule layer," it is still to be noted that an internal division of the external granule layer exists here which is free from granules, and has been named by Henle the external fibrous layer. It must be observed, however, that rod and cone fibres occur everywhere in the external granule layer, and therefore in that part also where the special name of external fibrous layer is not applied to it.

As the adjoining figure shows, the cone fibres are thicker

Fig. 349.

Fig. 349. Cone and cone fibre, the latter presenting varicosities, from the vicinity of the yellow spot of the retina of Man. Magnified 500 diameters.

than the rod fibres. Both are pale, with a smooth surface, and especially in the case of the thin rod fibres are very easily broken down. Their disappearance in dilute solution of chromic acid or of perosmic acid stands in direct relation with the above-mentioned occurrence of varicosities, since the more dilute the solution the larger do these become, and the fibres ultimately swelling in every part are destroyed.

These appearances agree completely with those we have observed in the nerve fibres of the retina. The thicker and somewhat more resistant cone fibres undergo similar metamorphoses to the rod fibres, the distinctness with which this may be seen being proportionate to their length; it is therefore most obvious at the macula lutea. When moderately hardened, they appear as pale perfectly smooth fibres which never branch, or anastomose, or pass into spongy plexuses, and are thus sharply differentiated from the radial supporting fibres and the connecting substance that surrounds them. In fluids in which the optic fibres exhibit strongly marked varicosities, distinct varicosities also usually occur in the cone fibres, leading ultimately to their complete swelling and solution (fig. 349). Lastly, they exactly resemble the thicker fibres of the optic layer, in the circumstance that, under high powers, they present

the appearance of being finely striated longitudinally, and therefore give some indication of being composed of fine fibrils, which we regard as characteristic of all the thicker axis-cylinders (fig. 350).

On reaching the external granulated layer, the cone fibres present a peculiar modification; each forming at the outer surface of this layer a conical triangular enlargement (fig. 348, 6), beyond which it is impossible to follow the fibre continuously.* These are so firmly imbedded in the substance of the external granulated layer as to give the impression that they are continuous with it. The cone-fibre spheroids, when isolated, have for the most part fragments of the granulated substance still adherent to them, supporting the view of their continuity. It is true that the conical enlargements in question here break up into fine fibrils, but these are different from those of the plexus. In successfully made preparations of the retina of Man, macerated in iodized serum, I have seen the conical enlargement break up into a brush of numerous and extremely fine fibrils, which were not joined together in a plexiform manner.† If we compare with this appearance that of the network of the external granulated layer, similarly hardened and isolated, the difference between the two kinds of fibres becomes exceedingly evident. This is further evidenced, on the one hand, by the ease with which the continuity of the plexus with the radial supporting fibres can be demonstrated; and on the other, by the manifold differences in appearance between the latter and the cone fibres, especially in the disposition to form varicosities, exhibited by the latter and the nerve fibres on their side, but which does not occur in the radial supporting fibres, whilst these, on the other hand, are characterized by their peculiarly rough surface. With these facts, the relation of the cone-fibre enlargement to the external granulated layer cannot, as is believed to be the

* H. Müller, *Zeits. für wissenschaft. Zoologie*, Band viii., Taf. i., figs. 1 and 3; Henle, *Eingeweidelehre*, p. 650; M. Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., Taf. xxxi.

† Hasse (*Zeitschrift für rat. Med.*, Band xxix., p. 252), believed that in all instances *three* of such fibrils emanated from each conical enlargement, whilst Merkel, *loc. cit.*, p. 7, considers that (at the macula lutea at least) a bifurcate division normally occurs.

case by W. Krause,* constitute a counterproof against the nervous nature of the cone fibres.

The rod fibres, again, can only be followed as far as, or just into, the external granulated layer. Our knowledge of their mode of termination is, however, still more imperfect than in regard to the cone fibres. The great delicacy and destructibility of the internal portion of the rod fibres in Mammals and Man only permit them to be exceptionally preserved throughout their whole course to the external granulated layer. Very frequently, and especially where numerous and large varicosi-

Fig. 350.

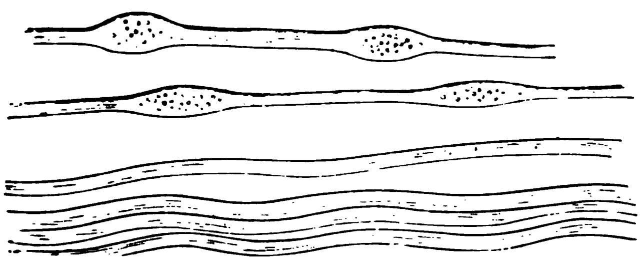

Fig. 350. Cone fibres, with and without varicosities, from the inner part of the external granule layer of the macula lutea of Man. Magnified 1,000 diameters.

ties appear in the course of the rod fibre, it terminates just above the external granulated layer with a clavate enlargement.† This gives the impression of being a *diminutive representative of the cone-fibre enlargement,* though I have not been able to observe any division of the rod fibres into the fine fibrils so characteristic of the cone-fibre spherule. In Fishes, however,‡ and still more in Birds and Amphibia,§ there is no doubt upon the point. The external granule layer in the last-named animals consists, for the most part, of only two layers

* *Membrana fenestrata.*

† Max Schultze, *Archiv für Mikroskop. Anatomie,* Band ii., Taf. x., fig. 1 ; Hasse, *loc. cit.,* p. 248.

‡ Max Schultze, *Archiv für Mikroskop. Anatomie,* Band ii., Taf. xi., figs. 8 and 9.

§ *Idem,* figs. 18 and 19.

of granules, which are connected with the external granulated layer by very short fibres. The rod granules and cone granules, and the fibres belonging to them, are here very similar, and break up at the outer granulated layer in the *same manner* into fine fibres. In Fishes, where the difference in the thickness of the more elongated rod and cone fibres is again very apparent, the conical enlargement of the rod fibres is also very similar to that of the cone fibres. In short, everything favours the view that no other essential difference exists between the rod and cone fibres than in their thickness, and that the rod fibre probably always breaks up into a number of fibrils at the external granulated layer, and thus also, like the cone fibre, is in reality a fasciculus of fibrils. In Mammals and in Man the rod fibres are very delicate, but are always several times thicker than the finest fibrils of the optic nerve. This is especially true of the external peripheric part which is turned towards the limitans externa, and which constantly and considerably exceeds the thickness of the internal central portion that extends from the external granule to the external granulated layer.

Every rod and cone fibre is connected with one of the so-called *external granules;* that is to say, each of these fibres has at some point in its course an enlargement in which a nucleus is imbedded, and this is named a rod or cone granule (see fig. 347). If the fibres in question are nerve fibres, the granules must be comparable to small bipolar nerve or ganglion cells. The quantity of the cell substance, however, is very small, yet still somewhat greater in the constantly larger granules of the cones than in those of the rods. The nucleus fills the interior of the granule almost completely, is of hyaline appearance, and contains a bright nucleolus, which is larger in a cone than in a rod granule. Except at the yellow spot, the rod nuclei are much more numerous than those of the cones; they are superimposed in several tiers upon one another, and are so closely arranged as to be in contact. The cone granules lie just beneath the membrana limitans externa, except where, as at the macula lutea, the cones are so closely placed that the granules belonging to them are necessarily in several layers.*

* Exceptionally in the more peripheric parts of the retina the interval

Thus it appears that the cone fibres are not, properly speaking, interrupted by the cone granule, but originate in it; for in most instances the cone itself is attached to the outer surface of the cone granule, whilst in the case of the rod granules, in consequence of their not lying immediately beneath the limitans externa, the connection of the rods is effected by a portion of the rod fibre, of similar nature, only somewhat thicker than the portion which extends to the external granulated layer. This last-named internal division of the rod fibre must obviously become shortened to a minimum, whilst the outer division must be proportionately elongated in those rod granules which are closely applied to the external granulated layer.

The rod and cone granules are perfectly transparent during life, the difference in the refractive power for light of the cell substance, nucleus, and nucleolus being scarcely perceptible; granular cloudiness becomes apparent in them after death, either in consequence of spontaneous coagulation, or owing to the action of reagents. In like manner it appears that the occurrence of transverse striæ or bands in the rod granules, described by Henle,* which can be observed sooner or later after death in Man and Mammals, and which may be rendered very distinct by the action of dilute acids,† is a *post-mortem* appearance depending on a partition of the nucleus or of the contents of the nucleus.‡

If the external granules represent a peculiar form of nerve cell introduced in the course of the nervous rod and cone fibres, the *rods* and *cones* themselves must constitute the nervous

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between the cone and the cone granule is also increased. The peripheric part of the cone fibre is then always thicker than the central part, extending from the granule to the granulated layer. (See below, fig. 355.)

* *Göttinger Nachrichten*, May and November, 1864, No. 7.

† Max Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., p. 219. According to W. Krause (*Membrana fenestrata*, p. 32), they may also be observed in the cone granules.

‡ W. Krause, *Anatomie d. Kaninchens*, p. 129. See also, in regard to the still unexplained appearance of transverse striæ, Ritter in Gräfe's *Archiv*, Band xi., Abtheil i., p. 89. G. Wagener (*Sitzungsberichte der Naturwissenschaft. Gesellschaft zu Marburg*, 1868, No. 5) remarks in regard to the transverse striation, that in fresh preparations it is more distinctly visible with low, than with high powers.

terminal organs of the optic nerve. The anatomical connection is perfectly clear, since it may be seen that each flask-shaped cone situated outside the membrana limitans externa is continuous with a granule, whilst each rod-fibre is continuous with a rod, which either springs directly from a rod granule,

Fig. 351.

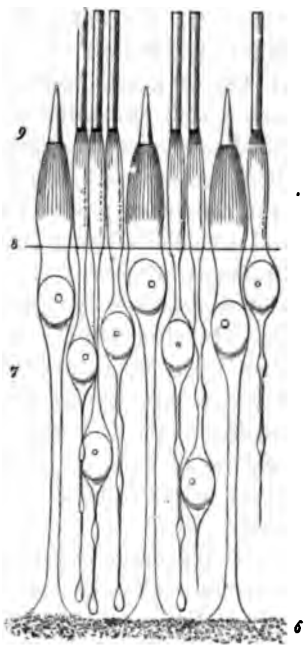

Fig. 351. From the posterior part of the retina of Man. 6, External granulated layer; 7, external granule layer; 8, limitans externa; 9, rods and cones, the external segments of which are sharply defined from the internal. Magnified 800 diameters. The supporting fibres of connective tissue are omitted in this drawing.

if the granule be placed just beneath the membrane, or if not, with the intervention of a thicker portion of the fibre. The layer of rods and cones thus covers like a wood of close-set palisades the outer surface of the external granule layer, and completes the formation of the retina as a nervous expansion. The conversion of luminous waves into nerve move-

ment, which is the fundamental condition of the visual act, must take place at this spot.

The *rods* are cylindrical bodies with a length at the back part of the eye in Man of fifty to sixty micromillimeters, and a thickness of two micromillimeters ; more anteriorly, near the ora serrata, they are somewhat shorter, though equally thick. They stand in close apposition, so that there is not much more space between them than results from their cylindrical form. Distributed at regular intervals between the rods, except at the macula lutea and the ora serrata, are the flask-shaped cones. The distance between two cones amounts on an average to eight or ten micromillimeters, the intervening space being occupied by three or four rods in a straight line. The average thickness of the cones at their base, with the exception of those of the macula lutea, varies from six to seven micromillimeters. Externally they diminish like a wine flask, and are not unfrequently slightly distended just above the base; they terminate in a conical point, the extremity of which is in a plane anterior to that of the rods, so that the cones are shorter than the adjoining rods. Like the rods, the cones also become shorter towards the ora serrata, and still earlier increase in thickness.

In both structures two essentially different segments are distinguishable, which have been named respectively the external and the internal segment, by W. Krause.* The distinction is most marked, and has been longest known, in the cones, in which the conical point characterized by its higher refractive power had previously been indicated by H. Müller as the cone-rod. The rods present a similar structure, except that the external segment is not conical in form, but for the most part regularly cylindrical.† The junction between the external and the internal segment in the rods of Man is situ-

* *Göttinger Nachrichten*, 1861, No. 2. *Zeitschrift für rat. Medicin*, Band xi., p. 175. 1861.

† In Amphibia only (Frog, Triton, Axolotl) does the diameter of the external segment of the rod slightly decrease towards the outer extremity. This is particularly observable in young animals (*Archiv für Mikroskop. Anatomie*, Band iii., Taf. xiii., fig. 14), and may in some instances render it impossible to distinguish the rods from the cones.

ated in the posterior part of the fundus, at about the middle of their length. I estimate the length of each segment in this region at about twenty-five or twenty-seven micromillimeters. The boundary line between the external and the internal segment of adjoining rods lies, for the most part, in one and the same plane. The plane of junction of the two segments in the cones, however, is different, being situated more anteriorly both in Man and Mammals. The inner segment of the cones (the body of the

Fig. 352.

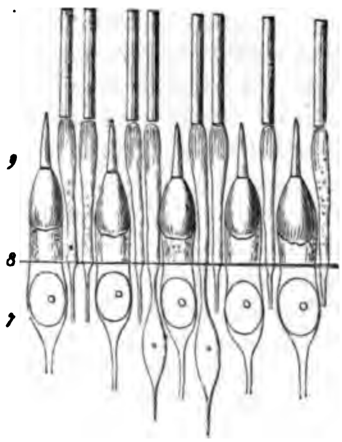

Fig. 352. Cones and rods, 9 ; limitans externa, 8 ; and part of the external granule layer, 7 ; from the posterior part of the retina of the Pig. Each of the cones, which are in very close apposition, contains in its inner segment a highly refractile body, the function of which is unknown. Magnified 800 diameters.

cone) is consequently always shorter than that of the adjoining rods; the difference in length between the inner segments of the rods and of the cones at the posterior part of the eye amounting in Man, upon the average, to six micromillimeters. On account of the great difficulties encountered in obtaining a view of the fresh and uninjured cones, it is by no means easy to ascertain their exact length. It appears, however, to be the rule that where rods and cones occur mingled together, the outer segments of the cones are *always shorter* than those of the rods. In Man I estimate the length of the conical outer

segment of the cones, which have been taken from the back part of the eye, and preserved as perfectly as possible, to be twelve micromillimeters. This is about one half of the length of the corresponding part of the adjoining rods. Great differences in this respect exist amongst animals. Thus, for example, in the Pig, the retina of which contains an extraordinarily large number of cones, the small length of the latter in comparison with the rods is very striking. At certain points the cones, with their external segments, scarcely reach the line of junction of the outer and inner segments of the rods. (See the adjoining woodcut.)

The difference in the refractive powers of the two segments of the rods and cones is apparent even in perfectly fresh specimens, but becomes still more distinct after death, coincidently with the occurrence of *post-mortem* changes that then rapidly take place, even with the most careful treatment. These changes consist partly in the originally homogeneous substance of the somewhat less strongly refractile internal segment becoming cloudy and finely granular, whilst the outer segment remains homogeneous and highly refractile. As a consequence of this, the line of junction of the two segments is rendered more distinct. Whilst the rods can be preserved for some time in indifferent fluids without undergoing further alteration, a process of coagulation usually occurs in the inner segments of the cones, rendering them coarsely granular and progressively more and more opaque, their outer segments soon becoming wholly unrecognizable. In these last alterations set in almost unavoidably immediately after the preparation of the fresh specimen, resulting in the arching and curvation of the whole structure with division into disks, which after remaining connected for some time ultimately become swollen up and disappear.

The same changes are undergone, though more slowly, by the outer segments of the rods. The peculiar alterations that have long been known to occur in them when floating in serous fluids, especially after dilution with water, and which have been regarded as a kind of coagulation, depend, as I have shown,* upon imbibition of fluid, which in the first instance produces

* *Archiv für Mikroskop. Anatomie*, Band iii., p. 224.

a very apparent and regular transverse striation, and leads quickly to a separation of the substance into disks. As the process of imbibition in many instances does not occur with uniformity, curvatures, crook-like archings, and various other alterations of form, are occasioned in the outer segment, the final result of which is a spheroidal body resembling certain myelin drops.

The larger rods of the fresh retina of the Frog, isolated in serum, always exhibit in parts a very fine transverse striation when examined with centric illumination and a magnifying power of from 500 to 800 diameters. When this is not at first observable, it can be rendered distinct by very oblique illumination.* As soon as swelling takes place in the substance of the outer segment, in consequence of imbibition, disks may be seen to separate, and these again undergo further change, especially in serum diluted with water, swelling up and becoming ultimately totally unrecognizable. The rods of the retina, both of Man and animals, undergo precisely similar changes. The highest powers of the microscope and very oblique illuminations are however indispensable at an early period, before swelling with prolongation of the external segment has taken place. The external segment of the rods of Man and Mammals which whilst still warm have been placed in a one or two per cent. solution of perosmic acid, and have been thus preserved absolutely unaltered in form, exhibit, when examined with a power magnifying 1,000 diameters and very oblique illumination, a striation which is as sharp as a hair line drawn on copper, and is about as fine as the markings of Nitschia sigmoides, which is one of the most difficult test objects to resolve amongst the Diatomaceæ. This would correspond to a distance between the lines of 0.3 to 0.4 of a micromillimeter. In the cones the disks are somewhat thicker.†

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* Max Schultze, *Archiv für Mikroskop. Anatomie*, Band v., p. 380. Note.

† Direct measurements may be found in Schultze's paper in the *Archiv für Mikroskop. Anatomie*, Band iii., p. 228, and in that of Zenker, *idem*, p. 259. By the application of a more perfect system of lenses, I now obtain somewhat smaller numbers than those given in the above. W. Krause's objections are contained in his *Essay on the Membrana fenestrata*, p. 23.

Besides this structure, so characteristic of the outer segments fresh or well-preserved specimens also exhibit a longitudinal striation.* This, as Hensen first recognized, depends upon the presence of a number of folds running in the direction of the long axis, or in elongated spirals which at the same time vary in depth. As it frequently occurs that in rods preserved in osmic acid, friction or pressure causes the separation of disks of varying thickness, which turn their flat surfaces to the

Fig. 353.

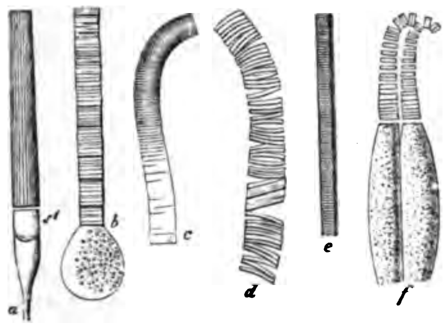

Fig. 353. Outer segments of rods and cones. *a—d*, Rods from the Frog; *e*, from Man; *f*, twin-cone from a Fish (Perch); *a*, fresh rod still connected with the internal segment (*s'*, lenticular body); *b*, first stage of imbibition in serum; *c*, the same stage in dilute solution of potash, magnified 500 diameters; *d*, disintegration of a rod into disks in serum, magnified 1,000 diameters; *e*, appearance presented by a rod from the retina of Man immersed in strong solution of perosmic acid immediately after enucleation, and macerated for twenty-four hours, magnified 1,000 diameters; *f*, fresh rod examined in serum.

observer, it is easy to obtain a clear image of the relief of the surface. In such disks, shown in fig. 354, besides the grooving of the surface, there is some indication of radial cleavage of the substance of the rod proceeding from the bottom of the grooves. Fresh rods examined in serum exhibit here and there longitudinal fissures. The appearances presented by the surface of the disks, which call to mind blood corpuscles, the edges of

* Hensen in Virchow's *Archiv*, Band xxxix., Taf. xii., fig. 7. Max Schultze, *Archiv für Mikroskop. Anatomie*, Band v., Taf. xxii.

which have become serrated, are not caused by a process of shrinking. The form of the natural transverse section of the outer segment in the fresh state is exactly the same. I have shown that the longitudinal striation, which is more easily seen in Amphibia and Fishes on account of the larger size of the outer segments, is also present in Man and Mammals, and here also probably depends upon a channelling of the surface. It is a highly remarkable circumstance that the transverse section

Fig. 354.

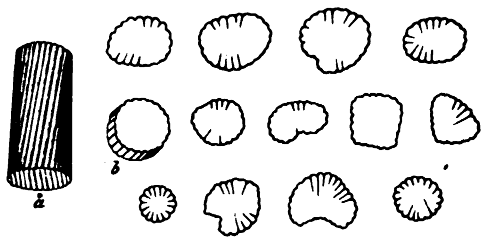

Fig. 354. *a*, External segment of a Triton examined in the fresh condition in serum; *b*, thin disk of the same, broken off after treatment with a two-per-cent. solution of perosmic acid, seen somewhat laterally. The remaining figures represent similar or even still thinner disks, seen from the surface, with fissures penetrating to a variable depth. Magnified 1,000 diameters.

of the large external segments of Amphibia (Triton) and Fish (Syngnathus) often differs considerably from the circular form, and may present an irregular dentated border, or even be of semilunar shape.

Several observers have expressed themselves in favour of the existence of an axis fibre running in the interior of the external segment. Ritter's* first description, as well as the corroborating observations of Manz and Schiess,† lead to the supposition that we are here dealing with appearances that owe their origin to the action of the preserving fluids; but if in a perfectly fresh Mammalian retina we obtain a surface view of

* Gräfe's *Archiv für Ophthalmologie*, Band v., Abtheil ii., p. 101, Taf. iv.

† *Zeitschrift für rationelle Medicin*, Band x., p. 305. 1860.

‡ *Idem*, Band xviii., p. 128. 1863.

the still well preserved extremities of the rods in their natural state, it will be found that, by careful focussing, a black point or short line becomes occasionally visible in the centre of the rods,* and this may be attributed to the presence of an axis fibre. Hensen† firmly maintains, in opposition to Krause,‡ that the appearance in question is really caused by a pre-existent structure. A perfectly satisfactory explanation of its occurrence has not yet been given; for no one has hitherto demonstrated the presence, by isolating it, of an axial fibre in the outer segment. It is to be observed also, that no trace of an axis fibre or of an axial canal can be discovered in the detached disks even of the thick rods of Amphibia, however perfectly they may be preserved. (See the above figures.) On the other hand, it must be admitted that, according to the observations of Zenker,§ there is a difference in the refractive index between the investing layer and the central portion of the rods, which in all probability furnishes an explanation of the appearance in question. These indices are estimated by Zenker to be 1·5 for the maximum, and 1·33 for the minimum. In the rods of the Frog,|| when slightly swollen in perosmic acid, Hensen believed he saw indications of the presence of three axial fibres lying in close apposition.¶

Hensen** also, with a few other observers, believes that an axial fibre may be distinguished in the *inner segment* of the rods. W. Krause†† first depicted this in the cones of Birds, when he made it terminate in an ellipsoidal body, to which he applied the term optic ellipsoid. We shall return to the consideration of these bodies when speaking of the rods and cones of Birds and other animals; nothing whatever of them can be distin-

* Max Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., p. 219, Taf. xiv., fig. 5. Hensen, in Virchow's *Archiv*, Band xxxix., p. 486, Taf. xii., fig. 4 *A*.

† *Archiv für Mikroskop. Anatomie*, Band iv., p. 347.

‡ *Membrana Fenestrata*, p. 23.

§ *Archiv für Mikroskop. Anatomie*, Band iii., p. 259.

|| Krause more recently estimates the refractive index of the rods to be from 1·45 to 1·47. *Membrana fenestrata*, p. 25.

¶ Virchow's *Archiv*, Band xxxix., p. 489, Taf. xii., fig. 8.

** *Loc. cit.*, fig. 6.

†† *Anatom. Untersuch.*, 1860, Taf. ii., figs. 5 and 6.

guished in the rods of Man or of Mammals. The existence of an axial fibre in the inner segment leading up to the ellipsoidal body like the supposed fibre of the outer segment, is however very doubtful. I have myself been unable to discover any axial fibre in the rods of Man.

The internal segments of the rods and cones in Man and many animals, on the other hand, exhibit, when very completely preserved in perosmic acid, and carefully examined with the highest powers, a fine *longitudinal striation on the surface,* * which recals that above mentioned of the *outer* segments of Amphibia, and is in fact, partially at least, continued on the latter.† Even if in these last, however, it is impossible to demonstrate that the striæ are independent structures by isolating them in the form of fibres, the impression given being due rather to simple channelling of the surface (see above), it is nevertheless certain that there are points at which fine fibrils producing the appearance of striation are capable of being stripped off the *internal* segments. In the large cones of the human retina, the striation of the surface is under certain circumstances very distinct. The striæ run longitudinally or in long spirals, and are from forty to fifty in number; they are placed at equal distances from one another, and this amounts at the widest part of the cones to about half a micromillimeter. At the apex of the internal segment they become so crowded, that with the optical means at present at our disposal it is impossible to distinguish them. Yet the impression is given that the striæ are continued in the form of a conical tube on the surface of the outer segment; for a delicate sheath proceeding from or continuous with the striated cortex of the internal segment may be isolated for a variable distance on the outer.

Like those of the cones, the inner segments of the rods of Man and of Mammals present a striated surface. The striæ, which are eight or ten in number, run in the form of extremely fine lines placed at equal distances around the internal segment, and parallel to its long axis, or, as in the cones, in elongated

* Max Schultze, *Archiv für Mikroskop. Anatomie,* Band v., p. 394, Taf. xxii.

† Hensen made the first observation on this point in the Frog. Virchow's *Archiv,* Band xxxix., p. 489.

spirals, as far as to the boundary line between the inner and the outer segments. If the latter have become detached whilst still well preserved in perosmic acid, it may be observed that fine fibrils which are continuous with the striæ of the internal segment project free from the end, forming a kind of basket by

Fig. 355.

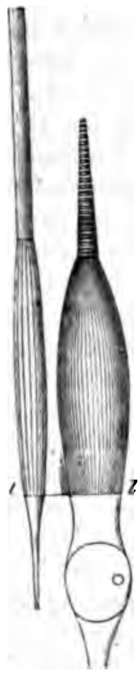

Fig. 355. Rod and cone from the retina of Man, preserved in a two-per-cent. solution of perosmic acid, to show the fine fibres of the surface, and the different lengths of the internal segment. The outer segment of the cone is broken up into disks, which, however, are still adherent to one another. Magnified 1,000 diameters.

which the outer segment was previously enclosed. In short, it may be said that here, as in the cones, a fibrous investment for the outer segment is formed from the striæ of the inner segment, and that this to some extent at least can be isolated. It is possible also, notwithstanding their delicacy, to perceive

extremely fine longitudinal lines running either in a straight direction, or in easy spirals, upon the highly refractile external segments of the rods of Man.*

As has already been stated, these fibres are capable of being partially isolated. At the base of the cones in particular they are easily separable for a certain constant length, and remain, forming by their continuity a short tube composed of stiff fibrils, seated on the membrana limitans externa, where the cones have themselves become detached from this membrane.† Examined from the surface, the limitans externa then appears to be finely punctated in circles, the diameter of which corresponds with that of the cones,‡ and gives the impression that the fibrils, of which we considered the cone fibres in the outer granule layer to be composed, here run separately upon the surface of the bodies of the cones. In this event the fibrils would be nerves. Nevertheless, this does not appear to be the case. The fine fibrils can only be followed backwards into the outer granule layer with very great difficulty. I have, however, ascertained this much with certainty, that they are continuous with the tissue *intervening between* the rod and cone fibres. As this can only be considered to be connective tissue, the fibres in question must represent a prolongation of the delicate and already finely fibrillated or striated connective tissue of the outer granule layer, and form to this extent isolable "*supporting basketworks*" or cradles for the bases of the cones and rods, § (see below, fig. 360). The further superficial relations of these fibres, especially in the case of the cones of Man, are rendered doubtful by a fresh complication of structure

* Max Schultze, *loc. cit.*, Taf. xxii., figs. 7—16.

† I have depicted very incomplete portions of these fibres in the *Archiv für Mikroskop. Anatomie*, Band ii., Taf. xi., fig. 13*a*, and they have been described by W. Krause, who has applied the term "needles" to them, as forming a distinct constituent of the retina. *Membrana fenestrata*, figs. 4, 5, 21.

‡ *Archiv für Mikroskop. Anatomie*, Band v., Taf. xxii., fig. 6.

§ Landolt has recently described, in the *Archiv für Mikroskop. Anatomie*, Band vii., p. 94, a sheath-like prolongation of the connecting substance over the rods in Amphibia, which must in all essential respects agree with the above-named "fibre-baskets" of the cones of Man.

in the interior of the body of the cones. For my observations show that we here find a compact mass of extremely fine fibres

Fig. 356.

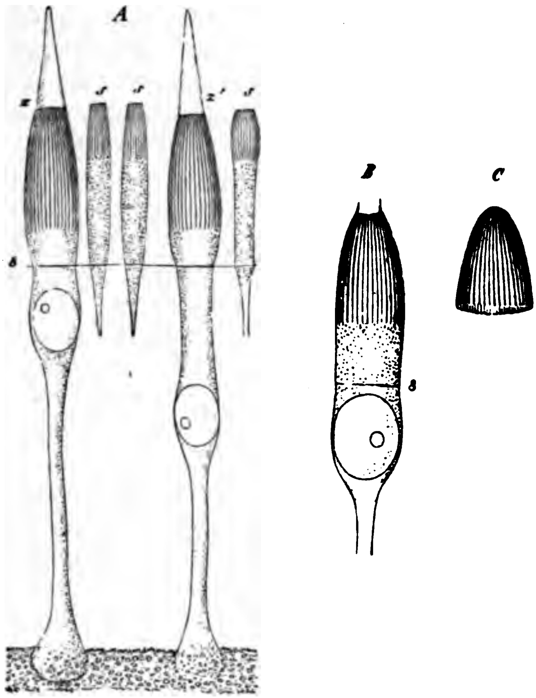

Fig. 356. From Man, showing the inner segments of the rods, *s s s*, and cones, *z z'*, the latter in connection with the cone granules and fibres as far as to the outer granulated layer, 6. The cone *z'* is characterised by an unusually long bridge between the body and the cone granule (the thicker peripheric part of the cone fibre). The fibrillar structure of the interior of the inner segments of the rods and cones is represented, magnified 800 diameters. *B*, Inner segment of a cone, with cone granule, and commencement of the cone fibre in which the inner fibrillar portion does not extend so far towards the limitans externa, magnified 1,200 diameters; *C*, isolated fibre-cone from the interior of a cone, still shorter than the preceding one, taken from a cone situated near the ora serrata.

running longitudinally, which occupy and form the entire substance of the body of the cone from the surface inwards, so that

no distinction has hitherto at least been made out between the superficial and the deep fibres. The internal fibrils (which I have already imperfectly depicted in the *Archiv für Mikroskop. Anatomie*, Band ii., Taf. x., fig. 8) do not extend quite down to the limitans externa, but cease abruptly at a certain distance from it. At any rate, they here become invisible, and if they extend any further towards the cone fibre, change their nature. Cones are found containing small spheroidal particles like fat drops at the point where the internal fibrils appear to cease, whilst there are others that have snapped across at this point. In the fresh condition the fibrillated portion of the cones appears as a brilliant strongly refractile body. By careful maceration the fibrils may even be isolated. They cease at the point where the outer segment commences. The connection of the outer with the internal segment appears also to be effected by a sheath investing the fibrillar substance.

I have been able to recognize a very similar structure, composed of short stiff fibrils, in the interior of the inner segments of the *rods* in Man (fig. 356, *A*, *s s*). The appearances presented are precisely similar to those of the cones, and corroborate the view, otherwise well established, that independently of the different thickness of the nerve fibres belonging to them, no essential difference exists between the rods and cones beyond that of form and size, and that thus these two forms of percipient elements are only modifications of a type common to both.

With the rods and cones we have arrived at the end of the expansion of the optic fibres in the retina, and if we now take a general view of the connection of the nervous elements of the retina of Man, as we are justified by our present knowledge in stating it, we find, in the first place, (see the adjoining schematic representation,) that the non-medullated nerve fibres of the optic layer are directly continuous with ganglion cells. At the macula lutea, where this connection is particularly obvious, all the ganglion cells are bipolar. The peripheric process is the thicker of the two, and enters the internal granulated layer, where it divides. In other parts of the retina the ganglion cells appear to be for the most part multipolar, in which case there is probably one central process given off into the

optic-nerve layer, whilst the remainder run peripherically into the internal granulated layer, where they become exceedingly attenuated by division. The nature and course of the fine ganglion-cell processes of the internal granulated layer resemble in every respect those of the finest primitive nerve fibrils of the grey substance of the cortex of the cerebrum. During their intricate course they form an extremely close-meshed plexus, and lie imbedded in the tenacious spongy connective tissue, which prevents their isolation for any considerable distance. There is consequently but little prospect that the communication of these ganglion-cell processes with the nervous fibres of the following layers will ever be demonstrated. In the layer of the inner granules, nerve fibres are found running perpendicularly to the surface of the retina. But at the macula lutea there are also oblique fibres. Each of these fibres is interrupted by a small cell, an internal granule, or a bipolar ganglion cell, the central process of which (that part of the radial nerve fibre which ascends from the internal granulated layer) is very delicate, whilst the peripheric is thick. This probably always loses itself by branching in the external granulated layer, which resembles the internal, and permits as little as the former the course of the fine nerve fibrils that pass through it to be exactly followed. From it the rods and cones arise, standing perpendicularly to its surface, except at the macula lutea, where they are oblique. The cone fibres arise by the coalescence of a great number of fine fibrils, each forming a large fasciculus of such fibrils, which resembles a thick fibre of the optic-fibre layer, and is continuous with the nucleated cone granule; this is a bipolar ganglion cell, the peripheric process of which is usually the cone body itself. If, as often happens, especially at the macula lutea, there is a long intervening space between the cone granule and cone corpuscle or body, this part, which constitutes the peripheric portion of the cone fibre, is again thicker than the other or central portion. The rod fibres are very much smaller than the cone fibres. Whether they also are composed of several fibrils cannot be determined from actual observation, though it is on various grounds probable. The peripheric part of the rod fibres, again, is far thicker than the centric; each one begins at the external granulated layer with a dilatation which

Fig. 357.

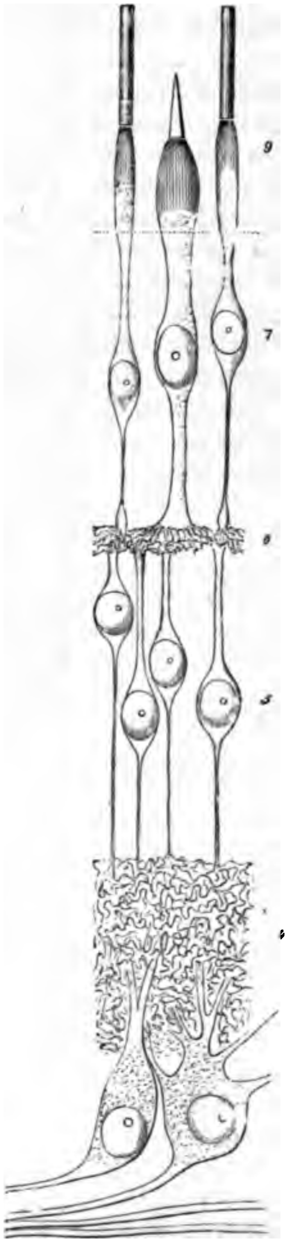

Fig. 357. Diagrammatic representation of the connections of the nerve fibres in the retina. The numbers are the same as in the diagram, fig. 344, p. 219. 2, Optic fibres; 3, ganglion cells; 4, internal granulated layer; 5, inner granule layer; 6, external granulated layer; 7, outer granule layer; 8, layer of rods and cones.

is comparable to that of the rod fibres, and is in many animals precisely similar. In the rods and cones themselves we see the terminal organs of the optic-nerve fibres. Whether the fibrils in the interior of the inner segments stand in connection with the nerve fibrils of the fibres in question, and form their modified extremities, must remain undecided, as well as the question of the relations of the outer segments to the nerve substance. It is highly probable that the internal and external segments have a common sheath or investing membrane, but that they are in any other way continuous, as, for example, by means of nervous fibres in their interior, is at present a pure matter of theory. Hence it is possible that the nervous substance may terminate at or in the internal segment, and the outer segment may represent a non-nervous physical accessory apparatus. The relation presented in fig. 357 appears to be very noteworthy and important for the explanation of the significance of nerve cells in general; namely, that the processes of the nervous cells of the retina always become thicker towards the periphery than towards the centre. If this difference in thickness depends on a difference in the number of the elementary nerve fibrils, the latter must become more numerous at the periphery than at the centre, which can only be explained by an augmentation of the number of fibrils within the nerve cells.

That the most minute peculiarities of structure presented by the rods and cones of the retina claim our attentive consideration, is obvious when we reflect that we have here to deal with structures that are capable of converting the undulations on which light depends into nerve force.

We may and indeed must suppose that the structure of the terminal organs is appropriate to their function, whilst the hope of discovering something artificial in the rods and cones is rightly grounded and supported on the fact that the more exact the research, and the sharper the definition of the instruments employed, the more delicate and the more remarkable are the details brought into view. No doubt but that many persons, in consideration of the extreme shortness of the waves of light, will regard this as too bold a statement. Yet if we bear in mind that the length of these waves amounts to 0·7 of a micromillimeter at the red end of the spectrum, and 0·4 at the violet end, which are

magnitudes that are not beyond the limits perceptible and measurable by the microscope, the statements above made will scarcely appear to be too venturesome. Comparative anatomical investigations will obviously prove of the very greatest value in this research. Whatever modifications the eyes of animals may present in regard to their structure and development, we may presume there is just such an agreement between the structure of the terminal organs of the nerves and the acessory apparatus, adapting them for the conversion of luminous waves into nerve force, as that which we see in the auditory organ, where delicate hairs—auditory hairs—project into a fluid. We shall here therefore endeavour to give a short *résumé* of the state of our information respecting the terminal apparatus of the optic nerves in animals, with a reference at the same time to the physiological value of the differences observed.

All Vertebrata that are able to see, with the single exception perhaps of the Amphioxus, the eyes of which present a much lower grade of development, possess a retina with a layer of rods and cones similar to that of Man. Now, although as a general rule the cones are recognizable by their *ventricose internal segment* and *conical outer segment*, and are mingled with rods, as in the retina of Man, there being no difficulty in distinguishing between the two either in him or in the Monkeys, Pig, Ruminants, and most Osseous Fishes; still cases occur in which the rods and cones resemble each other much more closely, as in the Guinea-pig and Rabbit, where the inner segments of the cones are scarcely thicker or in any other way unlike the rods, so that they can only be distinguished by the characters of their outer segments. Transitional forms are moreover seen in the Tritons* and in a less degree in the Frog, in both of which the outer segments of the rods are *conical*. In Birds the cones are very slender and rodlike. The external segment is much elongated, and is not always very distinctly conical. Though it would appear from this that the distinction between the rods and cones is not always sharply marked in the animal kingdom, there are nevertheless always other characteristics by which the two structures may be distinguished from one another. Amongst these special characteristics are the highly refractile spheroids of fatty substance found in the Birds, which for the most part have a red or yellow colour, and are present in all the cones, whilst they are absent in the rods. They are situated in the internal segment, at the point of its junction with the outer segment, and are so large, and so completely fill each cone at this point, that it

* Max Schultze, *Archiv für Mikroskop. Anatomie*, Band iii., p. 237.

is impossible for the light to reach the outer segment without traversing the spheroid in question. (See fig. 358, *z*.)

There are some colourless spheroids of this nature, but the majority are chrome, Naples yellow, gamboge, or greenish-yellow and orange, between which others are scattered at regular distances, of a ruby tint. Their spheroidal form must exert a refractile influence upon the course of the light traversing them, whilst certain portions of the rays corresponding to their colour must be absorbed. Their presence, as Hensen * first pointed out, renders it highly probable that it is by the external segments that perception is accomplished, since only in this case can the object of the selective absorption be understood. The circumstance that they are only present in the cones, and not in the rods, proves that the former have more to do with the perception of colour than the rods, which is also probable on other grounds for Mammals and Man.† That these spheroids occupy the whole thickness of the internal segment, demonstrates further, as Krause ‡ has stated, that we have here a solution of continuity, and that the outer segments are not of a nervous nature, even if this be true in regard to the inner segments. As a result of my discovery, that there are fibres running upon the surface of the internal segments, which are prolonged upon the outer ones, and are *not* interrupted by the fat spheroids, I believed that I might be able to point out the mode in which the outer segments take part in the process of perception. § The fresh complications, however, resulting from the discovery of the *internal* fibre system of the rods and cones, does not at present allow us to draw any definite conclusions upon the subject.

As in Birds, so also in Reptiles, oil globules are found in the cones; in the Chelonia, in addition to a few colourless globules, there are others that are red, orange, and yellow. Lastly, the very small cones of the Anourous Batrachians are each characterized by presenting a strongly refractive spheroid which is either colourless or of a clear yellow hue. They are not present in Fishes, unless we may consider them to be indicated by certain bodies observed by Leydig in the Sturgeon. ‖ Many of the cones in Birds (Pigeon) and Lizards contain besides the coloured spheroid some diffused red or yellow colouring

* Virchow's *Archiv*, Band xxxiv., p. 405.

† Max Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., p. 253.

‡ *Membrana fenestrata*, p. 48.

§ *Archiv für Mikroskop. Anatomie*, Band v., p. 400.

‖ *Anatom. Histologische Untersuchungen über Fische und Reptilien*, p. 9, 1853.

matter, which must consequently assist the selective absorption of the spheroids.

Moreover another structure adapted to exercise an influence upon the course of the luminous rays, is to be found in the internal segments of the cones in Birds, Reptiles, and Amphibia, and also in the rods of Birds and Amphibia; namely, a lenticular body of higher refractive power than the substance by which it is surrounded. This occupies the extremity of the inner segment in the rods, and is flattened posteriorly towards the outer segments, but anteriorly it presents a spherical or elliptic surface; in the cones containing spherical oil drops, it is situated immediately in front of and in contact with the drop. W. Krause first observed this body in the cones of the Fowl, and considered

Fig. 358.

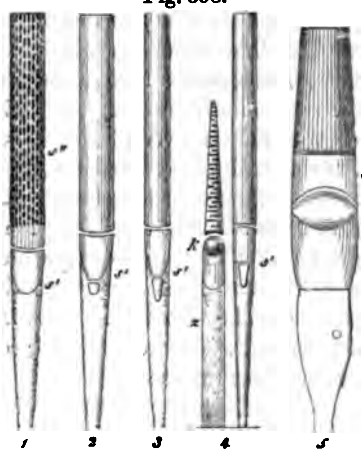

Fig. 358. 1, 2, 3, Rods of the retina of the Falcon : s', internal segment, with highly refractile lenticular bodies ; s'', external segment invested by lineally arranged pigment granules, as they may be seen to adhere to the surface of the outer segments in many specimens hardened in perosmic acid. 4, Rod and cone (z) from the Fowl : k, yellow flat spheroid in the internal segment of the cone, situated in front of which is an ellipsoidal refractile body. 5, Rod from the Triton : c, plano-concave ; c', biconvex lens in the internal segment. Magnified 800 diameters.

it must be regarded as the clavate extremity of a nervous central fibre of the internal segment, naming it at the same time the "optic ellipsoid." * I have termed it the lenticular body.†

* *Göttinger Nachrichten*, No. 37. 1867.

† Max Schultze, *Archiv für Mikroskop. Anatomie*, Band iii., p. 221.

Perosmic acid applied to the fresh retina of Birds and Reptiles brings out the lenticular body with extraordinary distinctness, preserving the sharpness of its outline, and at the same time scarcely altering its colour. No structure similar to this can be discovered in the cones and rods of Man, either in the fresh state, or when acted on by perosmic acid. It is particularly worthy of notice that in some animals the lenticular body of the rods is composed of two segments that react differently to this acid, and present also different refractive powers.* In the rods of Birds a small anterior segment often becomes separated from the point of the ellipsoidal lens, appearing in the form of a short pointed process, possessing a strong lustre † (fig. 358, *s*); and in Tritons the posterior segment presents a spherical concavity in front, in which the anterior segment lies (fig. 358, 5 *c*). We may reasonably suppose that we have here to do with arrangements which refract in a very definite way the rays of light passing to the outer segment.

The peculiar "*twin or double cones*," first described by Hannover, are quite enigmatical from a physiological point of view.‡ They have not up to the present time been discovered in Mammals or in Man,§ but they exist in Birds and Reptiles, Amphibia and Fishes. In Fishes, where they attain the largest size, and are the most numerous, and where consequently they are most easily examined, they consist of two apparently exactly similar coalesced cones, the outer segments of which, however, as well as the cone fibres, are separate and distinct, so that it might almost be said they were cones multiplying by longitudinal fission. It is different in other classes of animals; for, as I have shown, there are essential points of distinction between the two halves of the twin-cones, which must possess some physiological signification. In Birds, Tortoises, Lizards, and in the Frog, in which each ordinary cone contains a coloured or colourless globule, such a globule is found in only one of the halves of the twin-cones, the other half possessing merely the ellipsoidal lenticular body, which in many

* Max Schultze, *Archiv für Mikroskop. Anatomie*, Band v., pp. 401, 403, figs. 2 and 17.

† I formerly stated that this pointed body, as seen in swollen internal segments, might possibly be a persistent and resistant axis fibre. *Archiv für Mikroskop. Anatomie*, Band iii., p. 245, fig. 6.

‡ Hannover, *Récherches microscopiques*, etc., 1841. A more minute description of them, by Max Schultze, will be found in the *Archiv für Mikroskop. Anatomie*, Band iii., p. 231.

§ Hannover, indeed, believed he had found them in both Man and Mammals, but his observations were incorrect.

Birds is coloured yellow, but which even in them always presents an essentially different form and refractive power from the coloured oil globules of the other half of the cone.* Moreover there is often a difference in the length of the two halves, so that the one containing the oil globule extends farther back than the other; whilst the planes of junction of the outer and inner segments of the two halves do not coincide. If we regard the outer segment as the seat of distinct vision, there would be a necessity for different accommodation for the two halves of the twin-cones, supposing them to have the same function, and to receive the rays of light under otherwise identical conditions. This last, however, does not really occur, inasmuch as there is an essential difference between the refractile lenticular body of the internal segments of the two halves.

From all this we may draw the conclusion that the lenticular bodies are destined to give to the luminous rays a direction fitting them for undergoing their final changes in the outer segment, which, it would seem, cannot be given to them by the coarser refracting apparatus.

The *different distribution of the rods and cones met with in the animal kingdom* is well worthy of note. Both kinds of percipient elements can be replaced or represented by the other. Thus the cones are entirely absent in the retina of Sharks and Rays, the Lamprey (Flussneunaugen), and probably in the Sturgeon;† amongst

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* *Archiv für Mikroskop. Anatomie*, Band iii., Taf. xiii., fig. 6, *c*.

† The Petromyzon demands closer investigation than it has as yet received. In the river Lamprey (Flussneunauge) an opportunity presented itself long ago, in which I found that in the fresh condition it possesses only one kind of element in the bacillar layer, and these, on account of the form of their outer segment, I termed rods. According to a provisional communication by H. Müller (*Auge des Chamäleon*, p. 25), both rods and cones occur mixed together in the Petromyzon. In the Sturgeon, according to Bowman (on the Eye, p. 89) and Leydig (Fishes and Amphibia, p. 9), only one kind of percipient element is present, and these in Leydig's drawings resemble the rods in the form of their outer segments. In the osseous Fishes, rods and cones as a rule both occur. Amongst a large collection of Fishes of the Baltic which I examined in the fresh state in reference to the distribution of the rods and cones, and which included species of Pleuronectes, Gadus, Gasterosteus, Trachurus, Cottus, Crenilabrus and Syngnathus, I found in the latter genus alone any remarkable deviation from the ordinary type. The rods are here very thick and short as in Amphibia, the cones are much less conspicuous, and the disks into which the rods break up after short maceration in perosmic acid have in some instances a very well-marked semilunar form resembling that which I have described as occurring in the Triton.

Mammals, in the Bat, the Hedgehog, and Mole;* whilst the bacillar layer of the retina of many Lizards, Snakes, and Tortoises, and probably indeed of all Reptiles, is altogether destitute of rods, and is therefore *exclusively composed of cones.*† In Birds the number of cones is in general far greater than that of the rods, whilst in Mammals the reverse obtains. In the retina of Man and the Monkeys, as is well known, it is only at the yellow spot that the cones exceed the rods in number; at the centre of this acutely perceptive area the rods entirely fail. The retina of Birds resembles consequently the macula lutea of Man throughout its whole extent, in the relative proportion of the cones to the rods, and this similarity is still further increased by the circumstance that the yellow oil globules in the outer segments of the cones of Birds correspond to the presence of yellow pigment in the most sensitive area of the human retina. It is very remarkable that the number of the cones in the dusk or night-flying Owls is remarkably less, so that in these birds the rods again predominate, whilst at the same time the intensity of the yellow pigment in the cones is considerably smaller than in the day Birds, and the red pigment is wholly absent.‡ In Mammals that roam by night or in the twilight the proportionate number of the cones likewise diminishes, or they altogether fail, as in the Bat and other genera already mentioned. The cones in the Rat, Mouse, Dormouse, Guinea-pig, though present, are quite rudimentary as compared with those of Man, the Pig, Ruminants, and the Dog. Cats have distinct but slender cones; those of Rabbits are not so well marked.§

It is also a remarkable circumstance that the absolute length of the outer segments of the rods of most nocturnal animals is very considerable.‖ With the length of the outer segments, the *number* of

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* *Archiv für Mikroskop. Anatomie*, Band ii., p. 198, Band iii.; p. 238.

† *Archiv für Mikroskop. Anatomie*, Band ii., p. 209. The statement made by Krause, that in Lacerta agilis both rods and cones are present, is erroneous. Hulke, as I have shown, has not been able to distinguish the rods from the cones in Reptiles, so that his statements must be received with caution.

‡ See my statements in the *Archiv f. Mikrosk. Anat.*, Band ii., p. 208, the accuracy of which, after repeated re-investigation, I must still maintain, notwithstanding the opposition of W. Krause (*Membrana fenestrata*, p. 29).

§ Max Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., p. 197. For the conflicting statements of W. Krause, see his *Anatomy of the Rabbit*, p. 129, and *Membrana fenestrata*, p. 30.

‖ Max Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., p. 199, Taf. xiv., fig. 7 (Rat); p. 208, Taf. ix., figs. 10 and 11 (Owl); Band iii., p. 243. W. Krause, *Membrana fenestrata*, p. 31.

the disks placed one behind the other increases, whilst their thickness varies, though only to a slight extent. It would therefore seem that the refleetion and modifications of the luminous waves resulting from the disks, and having relation to perception on the part of the outer segments, must necessarily, from their greater length, be here much more complete. In correspondence with their entirely different mode of development, the structure of the retina of *Invertebrata* differs essentially from that of Vertebrata. This is particularly noticeable in the layer of the perceptive elements, or bacillar layer. In Mollusks, Articulate animals, and Vermes, the extremities of the optic nerve form, as in the Vertebrata, a layer of palisade-like structures. Apparently, however, these are more favourably placed in relation to the light than amongst the Vertebrata; they are directed forward towards the lens, whilst the bacillar layer in the Vertebrata is in contact with the choroid. This difference is explained by the mode of development of the retina in the two cases, being formed in the Vertebrata by an eversion of the central vesicle (see below), whilst in the Invertebrata it originates from an inversion of the skin.*

Amongst the Mollusca the structure of the retina is most exactly known in the Cephalopoda and Heteropoda.† The innermost layer of the retina, which is separated from the external layers by brownish-black pigment, is formed by rod-like palisades that are of considerable length in the Cephalopoda, and are visible even to the naked eye as a reddish lamina. The rod-like layer is composed—

1. Of lamellated palisades resembling the outer segment of the rods of Vertebrata, though much more variable in the form they present on transverse section, which may be semilunar, annular, quadrangular, or quite irregular. Adjoining palisades may so coalesce with one another as to form a continuous mass, traversed by vertical tubes. The laminæ that form these palisades, according to

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* Semper, according to a communication by Hensen, *Archiv für Mikroskop. Anatomie*, Band ii., p. 416.

† See Babuchin, *Würzburg. Nat. Zeitschrift*, Band v., p. 125, 1864; Hensen, *Ueber das auge einiger Cephalopoda*, "On the eyes of some Cephalopods," *Zeitschrift für wissenschaft. Zoologie*, Band xv.; and Bronn, *Klassen und Ordnungen der Thier. Molusken*, Taf. cxv. Steinlin, *Beiträge zur Anatomie der Retina*, St. Gallen, 1865-66, p. 70. Max Schultze, *Archiv für Mikroskop. Anatomie*, Band v., p. 1, *Ueber die Netzhaut anderer Mollusken*, "On the retina of various Mollusks," etc. Babuchin, *Sitzungsberichte der Acad. zu Wien*, Juni, 1865; and Hensen, *Archiv für Mikroskop. Anatomie*, Band ii., p. 399, in which last paper the literature of the subject is fully given.

my measurement, have almost the same thickness as in Vertebrata, *i.e.* about 0·5 of a micromillimeter.

2. In the intervening spaces between these palisades, and upon their surface, are fine fibrils, the extremities of the optic fibres. These, proceeding from a layer of nucleated fusiform bodies comparable to an external granule layer, enter the bacillar layer, whilst the nucleated fusiform bodies that terminate by one of their extremities in the fibres of the bacillar layer break up at their other extremity into fibrils which proceed from the optic layer.

3. In this layer the granular brownish-black pigment is also to be included. This is never absent at the outer extremities of the rods, and here separates these last from the fusiform bodies. This pigment, like the nerve fibres, lies external to the lamellated palisades which it invests, then extends further in the intervening spaces occupied by nerve fibres between the palisades, and frequently forms at the inner ends of the rods, where these are separated from the vitreous by a homogenous membrane, a dense accumulation filling up the spaces between the palisades. Light can penetrate into the latter, but is excluded by the thick layer of pigment from the canals containing nerve fibrils, or reaches these only by a circuitous path through the lamellar palisades.*

It is evident that if the fine fibrils running in Vertebrata upon the surface of the outer segments of the rods and cones are nerve fibrils, their position on the one hand in relation to the lamellated substance, and on the other to the pigment of the pigmented epithelial cells of the retina, would be precisely identical with that of the analogous structures of the retina of the Cephalopoda.

In the eyes of Articulata the structure of the retina is complicated in accordance with the circumstances of these organs, being here composed of many single eyes† united into one; but here also lamellated rods ‡ are found behind the refractile bodies comparable with the cornea, lens, and vitreous, with extraordinary powers of reflexion, and very often of considerable length. They also are invested by dark pigment, and stand in close relation to nerve fibrils, which enter at their posterior extremity, and terminate either

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* See especially Max Schultze, *Archiv für Mikroskop. Anatomie*, Band v., pp. 15—18.

† Leydig, *Das Auge der Gliederthiere*, "The Eyes of Articulata."

‡ Max Schultze, *Untersuchungen ueber die zusammengesetzten Augen der Krebse und Insecten*, "Researches on the compound eyes of Crabs and Insects." Bonn, 1868.

in them or at them. The lamination is here often recognizable with low power, as in the Crabs, since the finest disks do not here exceed 0·5 of a micromillimeter, and are united into groups that possess a different aspect, and in the River Crab can even be distinguished by their colour. The exact relation of the nerve fibrils to the lamellated rods is however less known in this case than in the Mollusks.

Finally, amongst the Vermes, at least in the large-eyed Alciope, the structure of the bacillar layer presents some analogy with that of the higher animals. The rods first observed by Krohn, so far as can be observed in my Neapolitan preparations preserved in various fluids, appear in the form of highly refractile, finely transversely striated, and easily transversely fracturing palisades, which are partly tubuliform, and anteriorly surrounded by pigment. In what manner the nerve fibres of the optic layer situated externally to the palisades terminate in this pigmented bacillar layer, is reserved for future research to determine.

It may here, however, be mentioned that recently much doubt has been expressed as to the rods and cones really constituting the terminal organs of the optic-nerve fibres. The rod and cone fibres may be of the nature of connective tissue, and may stand in connection with the connective-tissue cells and fibres of the internal layers of the retina. This opinion is maintained by W. Krause,* with whom Landolt† in a certain sense agrees, so far as regards the Amphibia. In Frogs, Tritons, and Salamanders, the external granule layer, as already stated, is so thin, and contains, besides the fusiform rod and cone granules, only such short fibres proceeding from these, that it does not appear to be by any means well adapted to settle the point in question. Landolt moreover admits that these fibres may contain nerve fibres in their *interior*. This is true also in the case of Birds and Reptiles. In Mammals and in Man, to which Krause's statements refer, the difference between the fibres of the connecting substance and those of the nerve fibres is, in accordance with the description given above, so great, whilst on the other hand the agreement of the rod and cone fibres with nerve fibres is so complete, that it is impossible on anatomical grounds to doubt the nervous nature of the rods and cones. Further researches are required to furnish an explanation of the reason why, after section of the optic nerve, as was first shown by Krause in animals, and in various cases of atrophy of the optic nerve and of the ganglion cells in Man, these bodies do not undergo degene-

* *Membrana fenestrata*, p. 48.

† *Archiv für Mikroskop. Anatomie*, Band vii., p. 84.

ration; but the fact of their persistence cannot shake the anatomically and physiologically well-grounded fact that the rods and cones represent the terminal organs of the optic-nerve fibres. The same argument also holds against the statements which have recently been made by Manz in a very valuable essay on the eyes of acephalous monstrosities against the nature of the rods and cones.* Their presence in hemicephalic fœtuses only proves that the elements of the external layers of the retina can under certain circumstances become developed independently of those of the inner layers, which, if the rods and cones are terminal nerve organs, is in complete accordance with that which is found in other nerves, the peripheric terminal organs of which may be found well developed when the central organs are absent.

2. The Pigment Layer of the Retina.

Although, so far as we know, not directly continuous with the nerve fibres, the *layer of pigment* cells, ordinarily termed the pigment epithelium of the choroid, still belongs, both physiologically and morphologically, to the retina. It is formed during the period of embryonic development from the outer lamina of the primary eye vesicle, which itself proceeds from a protrusion of the fœtal brain, and the inner layer of which is metamorphosed into the remaining layers of the retina. At a later period the rods and cones proceeding from the inner layer of the primary eye vesicle grow into the pigment layer, and thus the well-known and very intimate connection between the two is brought about.

The pigment cells resemble the hexagonal pieces of stone in a mosaic, united to form a membrane, the several cells of which however are still capable of being isolated. The external part of each cell adjoining the choroid is poor in pigment or perfectly colourless, and usually contains the spheroidal nucleus, as well as in many animals, the Frog for example, intensely yellow fat globules. The inner portion of the cells contains the peculiar granular colouring matter, and is prolonged in the form of numerous extremely destructible processes between the outer segments of the rods and cones, which last thus come to be imbedded in a pigmented sheath. These sheath-like processes

* Virchow's *Archiv*, Band li.

of the pigment cells break up at their extremities again into innumerable fine fibres, which are often quite colourless, and present no distant resemblance to a brush of cilia. They extend at least as far as the line of junction of the outer and inner segments of the rods and cones, and in many animals as far as to the region of the limitans externa. They closely embrace the rods and cones, but soon break down after death, owing to which the connection between the pigment cells and rods becomes less firm. After the perfectly fresh retina has been hardened in perosmic acid, the outer segments, even in Man, however, usually adhere so firmly to the pigment cells, that they rather separate from the internal segments, or fracture through their substance, than become detached from the pigment cells.

The intensity of the pigment varies; it is least in blonde individuals, greatest in the negro. It is always darker behind

Fig. 359.

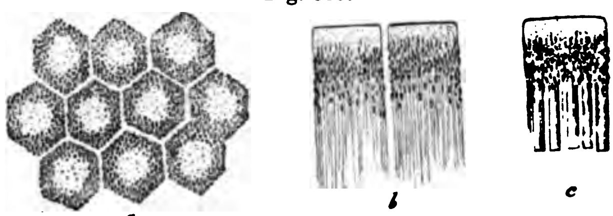

Fig. 359. Cells from the pigment layer of the retina of Man. *a*. Seen *in situ* from the surface. *b*. Seen in profile with the long hair-like processes partly pigmented, partly free from pigment. *c*. A cell also seen in profile, to which the outer segments of several rods are still adherent.

the macula lutea than in any other part of the retina. The retina of Albinoes is almost or entirely free from pigment, and it is absent in those parts of the retina of Mammals, where the choroid presents a highly reflecting tapetum. The hair-like ciliaform processes of the cells which invest the rods like a sheath are nevertheless well developed in these colourless cells.*

The pigment granules themselves, which appear for the most

* Max Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., Taf. xiv., fig. 9, *b*.

part to be not spheroidal, but *elliptical and rod-like*,* are, according to the statements of A. Frisch, small *crystals*, which when perfectly fresh are recognizable under very high powers by their sharp angles and borders.† They are placed with their long diameter at right angles to the surface of the retina, and therefore, when seen from this surface in profile, are of a rod-like form. Rosow and Frisch found that the largest measured from four to five micromillimeters in length.

The pathological pigmentation of the retina, known to ophthalmologists under the name of *Retinitis pigmentosa*, which is accompanied by diminished sharpness of vision, and leads ultimately to loss of sight, is highly remarkable. In typical cases of such pigmentary degeneration we have probably to deal with a partial degeneration of the pigment epithelium, and a more or less extended pigmentation of the other layers of the retina, together with a degeneration of the rods and cones, and finally with atrophy of the nervous constituents of the retina. The granular pigment set free by the breaking of some of the pigment epithelial cells makes its way into the other layers of the retina. This, however, is clearly only possible after previous destruction of certain parts of the bacillar layer and of the limitans externa, as well as of the external granule layer. Having reached the deeper layers of the retina, the granular pigment follows the adventitia of the bloodvessels, and thus probably the *perivascular lymph* sheaths, and thus becomes deposited far and wide in the form of diffused masses.

Inasmuch as this either occurs as a congenital condition, or takes place in early infancy as a result of hereditary influence, especially in the offspring of blood relations, who, as is well known, furnish a rich contingent of malformations, we may conclude that we have here a defective development in the outer lamina of the primary eye vesicle, which undergoes conversion (see below, "Development of the Retina,") into the pigment epithelium of the retina. Owing to the intimate relation existing between the pigment cells and the rods and cones, it is inevitable that processes of softening taking place in the pigment cells, and, implicating the bacillar layer, will by regressive extension also come to affect the other layers of the retina. Precise anatomical investigations upon this kind of degeneration, which has been admira-

* Rosow in Gräfe's *Archiv*, Band ix., Heft. iii., p. 65.

† A. Frisch, *Gestatten des Chorioidalpigmentes*, "Forms presented by the choroidal pigment." *Sitzungsberichte d. Acad. zu Wien*, 1869, Juli heft.

bly followed out ophthalmoscopically, are still only sparingly present.* In addition to this form of pigmentation, leading to impairment of vision, is another of a less serious nature, which consists in the development of stellate pigment cells (pigmented connective-tissue cells) in the supporting tissue and adventitia of the vessels, which is a frequent occurrence in animals, as has been particularly observed by me in the case of Ruminants.

3. The Connective-Tissue Framework of the Retina.

In addition to the nervous tissues that have hitherto been under consideration, almost all the layers of the retina are interpenetrated by a tissue occupying a considerable space in many parts, and this is *the supporting connective tissue.* Though continuous with that of the optic nerve,† it forms a very peculiar kind of framework in the retina, varying in its character according to the various nervous constituents of the several layers by which it is surrounded. This form of connective tissue is closely allied structually to that of the brain and spinal cord, and has, like it, been named Neuroglia by Virchow. We have applied the term "*spongy connective tissue*" to it, and distinguish as several parts belonging to it the *two limiting layers*—limitans interna and externa; the *radial fibrous bands,* or *supporting fibres,* in opposition to the radial nerve fibres; and the finer and coarser *plexuses* connecting the supporting fibres, which, from their resemblance to a sponge, have given their name to the whole tissue. The membrana limitans interna (limitans hyaloidea of Henle) immediately invests the vitreous humour, to which it is often intimately connected; whilst the limitans externa divides the layer of the external granules from the bacillar layer. Stretched between these two limiting layers, as columns between a floor and a ceiling, stand in great numbers the radial supporting fibres.

* Donders, in Gräfe's *Archiv,* Band iii., p. 139. Schweigger-Seidel, *ibidem,* Band v., Heft i., p. 96. Leber, *ibidem,* Band xv., 1869, Heft iii., p. 1. There is also an excellent illustration of the affection in Leibreich's Atlas, Taf. vi., fig. 1. Iwanoff describes, in Gräfe's *Archiv,* Band xi., Heft. i., p. 153, a deposition of pigment along the radial fibres.

† Klebs, Virchow's *Archiv,* Band xix., p. 321.

Whilst in all the layers of the retina these supporting fibres are continuous by means of lateral processes or branches with

Fig. 360.

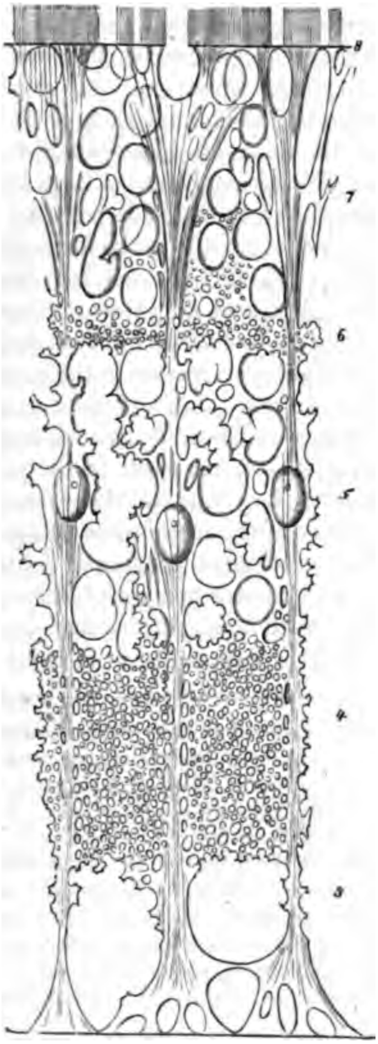

Fig. 360. Diagrammatic representation of the connective tissue of the retina, in correspondence with the characters it presents near the ora serrata. 1. Limitans interna; 3, ganglion-cell region; 4, internal granulated, or molecular layer; 5, internal granule layer; 6, external granulated or molecular layer; 7, external granule layer; 8, limitans externa, beyond which the cradles of fibres which embrace the bases of the rods and cones project. Magnified 800 diameters.

the intermediate spongy connective tissue, they are really merely a part of the same, and are distinguishable from it only

by a somewhat greater degree of resistance, permitting themto be isolated, whilst the intervening spongy tissue becomes broken down or destroyed. Small tags or fragments of the spongy tissue, or at least lateral processes, always remain attached here and there to the radial supporting fibres, and give rise to the peculiar and quite characteristic roughness of their surface. But the plexus, which, like a sponge, consists not only of fibres, but of membranous plates, forming shells and sheaths around the nervous elements, varies in thickness in accordance with that of the different layers of the retina, contains large spaces for the reception of the ganglion cells, smaller ones for the internal granules, and still finer ones for the nerve fibres of the two granulated layers.* The radial fibres are often seen to break up completely into spongy tissue, and thus it comes to pass that many of them which may be followed outwards from the limitans interna through all the layers, cease† in the external granulated layer, and therefore do not reach the outer granule layer. On the other hand, many radial fibres which may be followed into it from the outer layers, disappear in the plexus of the internal granulated layer.‡ Lastly, radial fibres may also be met with, which reach neither of the membranæ limitantes.

The radial supporting fibres are most constantly found in the internal granule layer. The greater number of them here also contain in their substance oval homogeneous nuclei, with distinct nucleoli. In general it is impossible to discover any

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* In opposition to the different views that have been advanced in regard to the structure of the young tissue of the granulated layers (see Henle and Merkel in the *Zeitschrift für rat. Med.*, Band xxxiv., 1869, p. 51, *et seq.*), I can only repeat what I have already stated in my *Untersuchungen über den Bau der Nasenschleimhaut*, ("Researches on the Structure of the Mucous Membrane of the Nose,") p. 29, Halle, 1862. I willingly admit that our microscopes and methods of preparation are insufficient for the investigation of the granulated substance of the cerebral cortex, but the spongy substance of the retina in the granulated layers is distinctly resolvable into a plexus of fibres, if due care be taken in its preparation, and if its examination be undertaken with our best immersion-lenses.

† Max Schultze, *Archiv für Mikroskop. Anatomie*, Taf. xiv., fig. 6, 8 *b*, 8 *c*, 10 *b*.

‡ *Ibidem*, Taf. xi., fig. 13.

granular protoplasm around the nucleus. These nuclei of the radial supporting fibres form the second kind of internal granules mentioned above. The supporting fibres themselves usually traverse the layer of optic-nerve fibres with great regularity, in order to take part in the formation of the limitans interna. They are here arranged serially, the direction and fascicular mode of grouping* of the fibres corresponding for the most part with that of the nerve fibres, whilst they are prolonged into conical flattened enlargements, or after undergoing division, like roots of a tree, are continuous with several such terminal dilatations,† which ultimately coalesce to form a smooth membrane on the side turned towards the vitreous—the frequently mentioned membrana limitans interna.‡ At many points the connection of the ends of the radial fibres with the membrane is deficient, in which case a fine fibrous plexus occupies the intervals between the truncated cones, and the limitans is perforated in a filigree-like manner. Such an appearance is presented by surface views of this membrane in Rabbits. At the yellow spot, where the optic fibres no longer form a special layer, and the ganglion cells occupy the inner surface of the retina, even the extremities of the thicker radial fibres fail to join the limitans interna. The radial supporting fibres are in point of fact commonly absent at this very soft portion of the retina; at the same time the limitans interna is by no means absent, but, on the contrary, is very resistant, and can easily be detached as a separate membrane. As in other parts of the retina, it appears as a denser membranous portion of the supporting connective tissue, but becomes detached from them and from the spongy substance between the ganglion cells, the more readily the greater the difference in the consistence of the two. The external surface of the limitans interna presents a very distinctly rough appearance at the yellow spot, owing to the remains of innumerable ruptured fibres, and demonstrates in this way its continuity with the adjoining portions of the connective tissue, which is at the same time doubtless very differ-

* Kölliker, *Gewebelehre*, 5th Edit., p. 680, fig. 488.

† M. Schultze, *De Retin. Structura penit.*, fig. 3.

‡ Schelske in Virchow's *Archiv*, Band xxviii., p. 482.

ent in character from the radially directed rows of fibres seen in the more peripherically situated parts of the retina.

Some differences of opinion prevail respecting the membrana limitans interna, which I believe depend on the different thickness and resistance it presents at various parts of the retina in Man and different animals, and its frequent coalescence with the vitreous. Kölliker* observes, in regard to this point, that the remarkable softness and destructibility of the radial fibres in contrast to the resistance of the limitans, is opposed to the idea of their identity of structure, and he consequently considers the limitans as a special tissue to be ranked amongst the vitreous membranes. In opposition to this, however, it may be remarked that other vitreous membranes, as the anterior elastic lamina of the cornea, or the internal layer of the choroid, also fuse with their supporting tissue, and may be held to originate with and out of this, though presenting essential differences in their relations to solvents. I am unable to discover any other kind of membrana limitans interna besides the above described, on which account I place its identity of structure with the supporting reticular or spongy connective tissue in the foreground, though fully recognizing the importance of the separability of the limitans, and the difference in resistance between it and the spongy subjacent layer, especially at the yellow spot. Henle also regards the limitans interna as an independent membrane, to the outer surface of which the radial supporting fibres, with their expanded extremities, are applied.† He calls it the limitans hyaloidea, to show that it is identical with the special membrane of the vitreous, described by many authors. The conditions of hypertrophy of the connecting substance which take place in atrophy of the nervous constituents of the retina are very instructive for the purpose of demonstrating the connection of the supporting fibres with the limitans interna, as they have been described in one case by Iwanoff,‡ where the hypertrophy of the radial fibres occasioned circumscribed enlargements extending into the vitreous.

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* *Gewebelehre*, 5th Edition, p. 681.

† *Eingeweidelehre*, p. 658.

‡ Gräfe's *Archiv*, Band xi., Abtheil i., p. 141, Taf. 3 and 4.

The limitans externa is not to be regarded as an isolable membrane. Like the interna, it is composed either of a membranous expansion of the radial fibres, or, where such isolable fibres are deficient in the granule layer, of the connective substance investing in manifold-wise the external granules, with their nerve fibres. The connecting substance of the outer granule layer is never absent,* not even at the macula lutea, where it was unobserved besides the long cone fibres, until Merkel demonstrated its existence in the form of delicate sheaths investing these fibres. (See his 'Macula lutea,' p. 7.)

Where, as in Birds, the radial supporting fibres can be readily observed to pass from the inner into the outer granule layer, each fibre may be observed to branch and form membranous capsules around the external granules and their nerve fibres. If after moderate hardening these granules, and with them the rods and cones, are removed as completely as possible by agitation from small fragments of the retina, the supporting tissue alone remains, forming a system of sheaths which only becomes in some measure intelligible on the application of very high magnifying powers. The sheaths themselves exhibit a fine parallel striation, indicating a *fibrillar* structure, which does not cease at the membrana limitans externa, which they help to form. For beyond the latter an indefinite number of fine stiff fibrils project (fig. 360, 8), which, grouped into the form of circles, form fibre-crates, cradles or basketworks, from which the cones fall out, as has been above described. The appearance presented is just as if these fibrils were continuous with the fibrous sheaths that invest the outer granules.† It was obviously portions of these fibrous crates which I formerly depicted‡ in specimens prepared from the Fowl as fibres exhibiting a certain connection with the connective-tissue sheaths of the external granule layer, and which were also described by W. Krause under the name of needles,§ who considered them to be a constant element of the bacillar layer. The illustration of M.

* W. Krause's *Widerspruch membrana fenestrata*, p. 19.

† See the illustration in the *Archiv für Mikroskop. Anatomie*, Band v., Plate xxii., fig. 4, from Man.

‡ *Ibidem*, Band ii., Taf. xi., fig. 13.

§ *Membrana fenestrata*, p. 6, Plate i., figs. 5 and 7.

Iwanoff, taken from a human retina, macerated by suppurative inflammation,* in which the nervous elements were collectively destroyed, whilst the supporting framework alone remained, exhibits similar appearances.

This fibrous basketwork, which is isolable in the above-described mode, appears to be present in all Vertebrata, as well as in Man. Further researches, however, are required to show how far it is prolonged over the surface of the outer segments.†

Besides the nuclei which are present within the internal granule layer in the radial supporting fibres, others are found, though for the most part more sparingly distributed in other layers of the retina, and especially in the two molecular layers.‡ The importance of these increases in those pathological processes which advance *pari passu* with an increase of the cells of the connective tissue. Even if the statements respecting a proliferation of these cells by fission are to be admitted with caution, it may nevertheless be regarded as established that under certain circumstances a finely or coarsely granular protoplasm containing fat molecules, collects around the pale oval nuclei of the connective substance, and that the number of these cells can augment materially in excess of all that we know of them in their normal state. Fatty degeneration of the retina does not limit itself to the immediate neighbourhood of the nuclei of the connecting substance, but may also, as for example in morbus Brightii, occur in the form of delicate rows of granules along the whole length of the supporting fibres, especially towards the inner layers of the retina, so that these fibres might be imagined to be hollow. In the *external* granule layer, also, I have observed cells that have undergone fatty degeneration, and which from the characters of their nuclei I must regard as elements of the connecting substance, so that it is impossible to deny the presence of nuclei of the connective substance under normal conditions in the external granule layer, however closely its nervous cells are compressed together. It is a matter of importance in regard to the question of the origin of those tumours of the retina that have been termed

* Gräfe's *Archiv*, Band xv., Abtheil ii., Plate ii., fig. 2.

† In an essay published in the 7th Vol. of the *Archiv für Mikroskop. Anatomie*, p. 81, E. Landolt maintains, on the ground of his personal observation, that in *Amphibia* the *outer segments* of the rods and cones lie in a sheath belonging to the supporting connective substance.

‡ See *inter alios Nagel* in Gräfe's *Archiv*, Band vi., p. 218.

glioma by Virchow,* to point out that one of their essential constituents coincides with the spongy substance (neuroglia), and that it may also proceed from the external granule layer.†

We are indebted to H. Müller for our knowledge of peculiar smooth stellate and anastomosing cells forming a double layer in the Perch and Ruff or Pope (Acerina cernua), which lie on the inner side of the external granulated layer (intergranule layer), and are not ganglion cells. They may be found in many other animals, though, perhaps, not always so easily isolable, and form, where they attain their greatest development, as in Fishes, a special layer lying to the inner side of the external molecular layer, to which I have given the name of the *stratum intergranulosum fenestratum*.‡ The substance of the nucleated laminæ anastomosing together by means of processes resembling sheets of perforated iron, frequently possesses the structure of striated plexiform (Plagiostomata), or fibrillar (Perca), connective tissue,§ and is often directly continuous, as I have shown, with that of the radial supporting tissue. In Perca fluviatilis I find this foraminated intergranular layer to be composed of three separate layers. The middle one includes the flat stellate cells, which frequently anastomose, but the processes of which may be as broad as the cells, so that the layer rather resembles a plexus of broad nucleated fibres. These are covered on one side by a plexus of delicate fibres resembling the branched and interwoven elastic fibres, which form a single layer of wide-meshed tissue. On the other surface is a thin lamina of apparently finely granular substance of great delicacy, containing scattered nuclei, and perforated by round holes.

W. Krause‖ has recently described the external granulated layer of the retina in Man and Mammals as being composed of

* *Vorlesungen über Geschwulste*, Band ii., p. 158.

† See Iwanoff in Gräfe's *Archiv*, Band xv., Heft ii., p. 84. Iwanoff clearly goes too far in maintaining that in no case can glioma develop from the external granule layer; for neuroglia—that is to say, spongy connective tissue—is, as I showed as long ago as 1859 in my treatise, *De Retinæ structura penitiori*, unquestionably present in this layer.

‡ *Zeitschrift für wissenschaftliche Zoologie*, Band viii., p. 17.

§ *De Retinæ structura penitiori*, p. 13, fig. 5, *f*, fig. 6.

‖ *Die Membrana fenestrata der Retina*, pp. 7—19. Leipzig, 1868.

a layer of flat cells of remarkably large superficial area. These cells, which anastomose by means of their processes, and thus form a fenestrated membrane, he considers to be at the same time in connection with the fibres of the rods and cones; the conical terminal enlargements of the latter being continuous with the substance of the cells, or of their processes. On the other hand, the radial supporting fibres which terminate at the limitans interna, end in this fenestrated membrane, and never reach the limitans externa. The holes of the membrana fenestrata are occupied by peculiarly formed internal granules, which, according to Krause, are the terminal cells of the optic fibres, with which, therefore, the rods and cones are not continuous, since these pass by means of their fibres into the fenestrated membrane formed by the connective tissue. I am unable to bring the results of my researches into harmony with these views.

Lastly, the bloodvessels of the retina, which in Man are distributed through all the inner layers, as far as to the external granulated layers throughout the whole extent of the retina, with the exception of the fovea centralis, are to be included amongst the connective tissue. The connection of their external walls with the reticular connecting substance resembles that observed in the lymphatic and lymphoid glands. Perivascular lymphatic passages are, as His supposed,* probably here present. The course of the vessels is elsewhere given.

4. Macula Lutea and Fovea Centralis.

The elementary parts of the retina that have now been described undergo essential modification in their form and arrangement at the macula lutea and fovea centralis in Man and Quadrumana. Nearly in the axis of vision, and at some distance to the side of the optic-nerve entrance, an *intensely yellow pigment* is deposited *between* the elements of the different layers, with the exception of those of the bacillar and external granule layers. The centre of the yellow spot is depressed on the surface looking towards the vitreous, to form the

* *Verhandlungen der natur. Gesellschaft. zu Basel*, Band iv., Heft ii., p. 256.

fovea centralis. The colouring material, which is most intense in the fossa, and becomes gradually paler towards the margin of the spot, does not present a granular appearance, but is completely hyaline, and in consequence only so far disturbs the transparency of the retina at this part, that it absorbs a considerable portion of the violet and blue rays before these reach the layer of cones.*

With the aid of Browning's spectroscope I have very distinctly perceived the shortening at the violet end of the spectrum under the microscope. I have not, however, by this mode of observation discovered any special absorption-bands. According to Huschke,† the intensity of the colour of the yellow spot is subject to variation, being brighter in blue-eyed than in dark-eyed men.

The retina is thicker at the macula lutea, of course excepting at the fovea centralis, than in the adjoining parts; but is at the same time softer and more prone to *post-mortem* changes. It is probably owing to its greater capacity for imbibition, that it usually swells up at this part soon after death, forming the so-called plica centralis. It is well known that the attenuated centre of the yellow spot tears with great facility, and then appears as a hole in the substance (Foramen centrale). The high degree of softness and destructibility of the substance of the yellow spot receives explanation from the circumstance that the delicate nervous elements far preponderate in this part over the widely distributed plexuses and fibres of the supporting tissue found in other parts of the retina. The nervous elements are very numerous and closely packed at the macula lutea, which is in accordance with its physiological importance as the most sensitive spot of the retina. The layer of the ganglion cells and internal division of the external granule layer, which Henle designated external fibrous layer, are the layers that are most obviously thickened. On the other hand, there is no continuous layer of nerve fibres beneath the limitans

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* According to Preyer (Pflüger's *Archiv*, Band i., p. 299), the first observations on this point were made by Maxwell. See also Max Schultze, *Ueber den gelben Fleck der Retina.* Bonn, 1866.

† *Eingeweidelehre* in Soemmering's *Anatomie*, p. 727.

interna. In the percipient layer the rods already begin to fail, even at the outermost edge of the macula lutea, their place being taken by the cones, and they ultimately altogether disappear. The cones, which are closely arranged, become more and more slender towards the border of the fovea centralis, so that they here resemble the rods. Thus it comes to pass that in the fovea a much greater number of cones find room than in any other corresponding area in the vicinity. The thickness of the cone fibres which are attached to the slender cones of the fovea centralis, and traverse the external granule layer, is, however, not much less than that of the thick cones of the more peripheric parts of the retina. Each slender cone of the fovea terminates also in as large a number of primitive nerve fibrils as the thick cones of the periphery.

The arrangement of the cones at the yellow spot is surprisingly regular.* They are disposed in curved lines, which converge towards the centre of the yellow spot, and produce the appearance of shagreen, or that presented by the engine turned back of many watches. This arrangement, which on physiological grounds had been predicted by Hensen,† is perfectly regular, the cones successively diminishing in diameter from the periphery of the yellow spot to the margin of the fovea; at this point, however,—that is to say, in the fovea itself,—the curves are less regular, and the cones in an area of about 0·2 of a millimeter in diameter are all of equal thickness.

As the thickness of the cones diminishes towards the fovea, their length increases. The outer segments, which at the more peripheric parts of the retina are concealed amongst and are somewhat shorter than the rods, become at the yellow spot, where they gradually supplant them, equal to or even longer than the rods, especially when, as in the fovea, the remaining layers of the retina retreat somewhat towards the vitreous, as though in order to make room for the longer cones.‡ In one case I found the longest cones above 100 micromillimeters in

* Max Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., Taf. xii.

† Virchow's *Archiv*, Band xxxv., p. 403.

‡ Max Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., p. 229, Taf. xiii., fig. 1.

length. H. Müller and Hulke have also found that the cones of the fovea are longer than those of the rest of the yellow spot.* The thinnest cones of the fovea are 3 μ in thickness at their base. These are distributed over a circular area of about 200 μ in diameter, which, as has been stated, is the diameter of the fovea centralis, if this be determined by the extent of distribution of the smallest percipient elements. Taking several diameters of this area, and in the perfectly fresh retina of Man, I counted in each fifty cones, all of equal slenderness. According to this, each cone would have a thickness of about four micromillimeters; but the fine intervening spaces between the cones ought to be deducted. In hardened specimens, measurements made of isolated cones often appear under three micromillimeters. In specimens preserved in alcohol, Henle found that they did not exceed two micromillimeters. Welcker, to whom we are indebted for some very exact measurements of these elements from the examinations of the retina of a criminal, estimated the thickness of the cones of the fovea between 3·1 and 3·6 micromillimeters, or upon the average 3·3.† The long conical external segments, as they run outwards to the choroid, become attenuated to one micromillimeter or less. They are invested by the pigment sheaths of the coloured cells of the pigment layer, which are for the most part darker at the macula lutea than in the adjoining part of the retina, and reach as far as the uncoloured outer part of these cells. We are in consequence probably able to perceive in Man, as I have already diagrammatically represented in an earlier work ‡ in animals, and especially in Birds in the perfectly fresh macula lutea, still covered with undisturbed pigment cells, the natural extremities of the cones as bright spots surrounded by dark pigment.

As already stated, no remarkable difference is observable in

* Hulke, *Philosophical Transactions*, 1857, p. 110.

† *Zeitschrift für rationelle Medicin*, Band xx., p. 176, 1863. For other measurements the reader may be referred to Max Schultze in Reichert and Dubois-Reymond's *Archiv*, 1861, p. 784, and H. Müller in the *Würzburg. Nat. Zeitschrift*, Band ii., p. 219, 1861.

‡ *Archiv für Mikroskop. Anatomie*, Band ii., Taf. xii., fig. 1.

the size of the external granules, or in the thickness of the cone fibres between those of the area of the macula lutea in question, and the more peripheric regions of the retina. On the other hand, the course pursued by the cone fibres is quite different. From the date of Bergmann's observations on this point it has been known that in the external granule layer, and especially in the subsequent inner division of this layer, which contains no cells, but free fibres alone, the course of the fibres even external to the borders of the macula lutea, change from a radial to a horizontal direction, which, coincidently with the thickening of this layer towards the border of the fovea, becomes constantly more and more oblique, so that in fact some fibres even run parallel to the surface of the retina. The rod and cone fibres, and afterwards the cone fibres alone, form curves which, prolonged backwards, all diverge from the fovea or from the visual axis, which if prolonged would pass through the fovea, and thus reach the outer granulated layer; though not by that shortest path which is pursued by the more peripheric fibres of the external granule layer. In consequence of the gradual and necessary prolongation of the cone fibres, a layer of horizontal fibres is produced, extending for some distance around the fovea, the beginnings and endings of which are no doubt radially directed; but which at a certain plane stream out like radii from the central fovea.* The explanation of this is found in the very existence of the fovea. At this point all the layers of the retina, with the exception of the cones and external granules, diminish to a minimum. The cone fibres of this region, in order to reach their destination, must diverge from one another in all directions. Beyond the fovea are the internal granules belonging to them, the internal granulated or molecular substance, and the ganglion cells. But from the uninterrupted cone layer fresh masses of cone fibres still come in order to seek their connections. And, although the ganglion-cell layer becomes considerably increased in thickness at the macula lutea, this is not the case with that of the internal granules. The fibres thus press outwards, till ultimately external to the yellow spot the direct radial course of the

* Merkel, *loc. cit*, Taf. i, fig. 11.

Fig. 361. Diagrammatic section through the macula lutea and fovea centralis of the retina of Man. Magnified 110 diameters. 2, optic-nerve fibres; 3, ganglion cells; 4, internal granulated layer; 5, internal granule layer; 6, external granulated layer; 7a, external fibrous layer; 7, external granule layer; 9, rods and cones; 10, pigment layer.

cone and rod fibres, such as they pursue in other parts of the human retina, and in the retina of animals that do not possess a fovea centralis, is re-established. An oblique direction, as Hulke has observed, is pursued also by the nerve fibres of the internal granule layer. In transverse sections carried through the macula lutea and fovea centralis, I found that the rod and cone fibres pursue an oblique course outwards on every side from the fovea for two millimeters in the horizontal meridian, but only for about 1·5 millimeters in the vertical meridian. According to Rud. Schirmer's observations on the ophthalmoscopic appearance of the macula lutea in healthy eyes, it is always of a tranversely oval form; its horizontal in relation to its vertical diameter being as 4 : 3.* The ganglion cells of the yellow spot are for the most part bipolar, as has been stated by various observers, and recently by Merkel.

The connective substance at the yellow spot, as has been already mentioned, is particularly tender and delicate, and has no thick radial supporting fibres. On the other hand, the membrana limitans interna becomes quite thick and strong. According to Merkel, it attains a thickness of three micromillimeters, though it again becomes attenuated at the fovea centralis. It separates with extraordinary facility from the delicate spongy connective tissue that occupies the interspaces between the ganglion cells.

A macula lutea and fovea centralis are only present in Quadrumana amongst Mammals, but here entirely agree in their anatomical characters with the corresponding parts in Man. Remak and H. Müller‡ have pointed out the existence of an area centralis, with a structure similar to the yellow spot in the retina of several Mammals; but we possess no precise information on the point. That in the retina of some Birds, not only one, but two fossæ are present at some distance from each other, was discovered by H. Müller,§ though he gave no details in regard to the principal elements of these parts. According to my

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* Gräfe, *Archiv*, Band x., 1, p. 150.

† Max Schultze, *Sitzungsberichte der Nieder-rheinische Gesellschaft zu Bonn*, Juli, 1861.

‡ *Würzburg naturwiss. Zeitschrift*, Band ii., p. 140, 1861.

§ *Loc. cit.*, and in his treatise *Ueber das Auge des Chamäleon*, p. 11.

observations, the percipient elements in the two fossæ centralis of the Falcon consist of cones of smaller thickness than in the adjoining parts, which possess only yellow, but no red pigment spheroids, though both are present in the other portions of the retina. The rods are entirely absent.* The retina of the Chamæleon presents a very well-marked fovea, the minute anatomy of which has been given with great exactness by H. Müller† and Hulke.‡ As appears to be the general rule in Reptiles, cones alone are found in the percipient layer of the entire retina of the Chamæleon. These, however, in the fovea centralis are only about one-fifth as thick as in the peripheric regions, but at the same time are much longer, so that the line of the limitans externa is here more distant from the choroid, just as I have depicted it in Man. To these cones, obliquely running cone fibres are attached, also closely resembling those of Man. But, whilst in Man the connective tissue of the external granule and cone fibre layers follows these fibres, H. Müller has demonstrated the presence in the Chamæleon of a peculiar kind of radial supporting fibres, which decussate at an acute angle with those of the cones. The delicacy of the individual cones of the Chamæleon, as seen in preserved eyes of this animal, surpasses that of every other animal.

In other Reptiles, as in Ophidia and Chelonia, it appears from the statements of Knox and Hulke,§ that a fovea is present, though not very well marked. On the other hand, in Amphibia and Fishes no indications of either a macula lutea or of a fovea centralis have been observed.

I have directed attention to the circumstance that the yellow screen, which in the macula lutea is situated in front of the percipent elements, must exercise an important influence on the amount of violet and blue that we see in the spectrum,‖ and it naturally suggests itself, that an increase in the intensity of the yellow pigment of the retina must produce yellow vision, or violet blindness. In considering the effects of santonin, I overlooked, as I here desire to be particularly noted, the fact that objects appear yellow, not only by direct, but

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* *Archiv für Mikroskop. Anatomie*, Band ii., p. 206.

† *Würzburg naturwiss. Zeitschrift*, Band iii., p. 10, 1862.

‡ *Journal of Anatomy and Physiology*, No. 1, p. 104, 1866.

§ *Loc. cit.*, pp. 103 and 104.

‖ See my treatise above cited, *Ueber den gelben Fleck der Retina; seinen Einfluss auf normales Sehen und auf Farbenblindheit.* ("On the yellow spot of the Retina: its influence on normal vision, and upon colour-blindness.")

also by indirect vision. I therefore retract my earlier view, which I consider to be no longer tenable. We, however, habitually see through another yellow screen present throughout *the whole extent of the retina*, namely, the *narrow-meshed plexus* of its *capillary vessels*, which lie *in front of* all the percipient elements, that is to say, between the limitans interna and the external granulated layer. The quantity of the rays of the spectrum which a single layer of corpuscles sometimes standing on their edges, and disposed like rouleaux of coin, absorbs is very considerable, as an examination with Browning's spectroscope shows. The hœmoglobin lines are visible, and a considerable portion of the rays at the violet end of the spectrum are lost. With thicker layers of blood corpuscles, like those circulating in the larger retinal vessels, the absorption effects would clearly be much more considerable. And, although there are many holes in this screen of bloodvessels through which we may see, and of which, on account of the constant movements of the eye, we are unconscious; yet the plexus of bloodvessels, especially if it be projected from the various layers of the retina into one plane, is too thick for its influence to be entirely disregarded. Alterations in the blood affecting this absorption power for certain luminous rays must necessarily lead to unusual perceptions of colour.*

5. Ora Serrata and Pars Ciliaris.

The neighbourhood of the ora serrata of the human retina, in opposition to the area surrounding the macula lutea, is characterized by the gradual disappearance of the nervous elements, whilst the connective tissue, on the contrary, is progressively more and more developed. The radial supporting fibres, with the spongy network connecting them, form the principal portion of the tissue at the ora serrata; and ultimately, though in a somewhat modified condition, appear to constitute that continuation of the retina over the ciliary processes which no longer participates in the perception of visual images.

H. Müller has made such extensive researches upon this subject, that little remains for subsequent inquirers to add. His results show essentially that the "several layers of the retina

* *Zeitschrift für wissenschaft. Zoologie*, Band viii., p. 91.

have undergone such diminution in the vicinity of the ora serrata, that their united thickness only amounts to 0·12 to 0·14 of a millimeter. The nerve and ganglionic spheroids become very sparingly scattered, so that they can only be found quite isolated between the internal extremities of the radial fibres; the granular layer, in consequence of the preponderating amount of the latter, has likewise become more vertically striated, so that ultimately its inner boundary disappears. The internal granule layer consists of only two or three not very closely arranged tiers of granules, and not unfrequently simple nuclei appear to occupy their place in the fibrous mass which extends through the slender intergranule layer to the external granules. The rods and cones are distinct, though they have become somewhat shorter. Just before the point of greatest attenuation, the retinal layers severally lose their peculiar characters to a still greater degree, and pass into an obscurely vertically striated mass, in which numerous roundish or oval nuclei are distributed. The bacillar layer is alone excepted from this general fusion or indifference of tissue, remaining to the last a separate layer, the elements of which rapidly diminish in size, and finally cease. As soon as this takes place the remaining layers form a *single tier of cells*, which constitutes the pars ciliaris, and is the immediate prolongation of the retina proper. The cells resemble in general those of columnar epithelium, but vary in height in different animals. H. Müller examined this region, particularly in the Pig, Ox, Rabbit, Pigeon, and Fowl. In the Rabbit their height amounts to 0·025 of a millimeter." H. Müller regards these cells as a continuation of the indifferent supporting apparatus of the retina, "whence, as it appears, the inner extremities of the radial fibres are perhaps to be reckoned as belonging to such of the inner granules as correspond to the—in most animals—distinctly different nucleated radial fibres . . ." Moreover the form of the cells in question is in some parts in Man such as to render their epithelial nature doubtful. They are isolated, frequently not rounded at the extremities, but provided with one or with several dentations and short processes, which are given off also from the longer side, so that they might be considered to belong to the group of connective tissues, against

which view the rounded cell forms occurring elsewhere certainly constitute no objection. Kölliker* completed these observations in so far that he directly states he has seen the gradual transition of the shortened radial fibres into the cells of the pars ciliaris. He admits also the presence of a membrana limitans interna at this part. On the other hand, we miss an exact description of the isolated cells, the forms of which, as H. Müller has already pointed out, may, owing to the presence of processes and dentations, be very various, and respecting which Klebs† from his investigations admits that they pass directly into the fibres of the zonula. Two regions, however, are to be distinguished here, the smooth posterior and the plaited anterior division, the plaits or folds of the latter forming the processus ciliares. Schwalbe‡ respectively designates these two the zone of the orbiculus ciliaris and the zone of the ciliary processes. He was able to isolate a limitans interna in both; but at the zone of the ciliary processes, after removal of the vitreous, he found that it remains in part adherent to the zonula Zinnii, especially at the points corresponding to the depressions between the processes, which also remain covered with the cells of the pars ciliaris retinæ and the pigment, in consequence of which the well-known form of the black-rayed zonula originates. Schwalbe, however, does not, like Kölliker, consider that the membrana limitans interna arises from the cells of the pars ciliaris, but describes it—together with certain reticular external processes, observed also by Merkel,§ which extend between the cells of the pars ciliaris, and correspond to the radial supporting fibres—as a prolongation of the connecting substance of the retina.‖ By this means the transition of the radial fibres of the retina into the cells of the pars ciliaris, which Kölliker considered to be an ascertained fact, is again rendered doubtful.¶

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* *Gewebelehre* Aufl. v., p. 685.

† Virchow's *Archiv*, Band xxi. p. 187, 1861.

‡ *Archiv für Mikroskop. Anatomie*, Band vi., p. 326.

§ *Die Zonula ciliaris*, Taf. i., fig. 9. Leipzig, 1870.

‖ *Ibidem*, p. 303.

¶ See also the essay of Manfredi, *Sulla struttura della parte cigliare della Retina*, in the *Gaz. Med. Ital-Lombard*, Ser. vi., Tom. iii., 1870.

According to my observations made on fresh human eyes which had been preserved for twenty-four hours, or for a somewhat longer period, in solutions of perosmic acid of various degrees of concentration, the cells of the pars ciliaris offer very diverse appearances. In general they form elongated prisms resembling tall columnar epithelial cells. At their outer extremities they are smoothly truncated, and are in contact with a pigment cell; at their inner extremities they either become enlarged or attenuated, and cleave firmly to the surface of the vitreous, which is here distinctly fibrous (zonula Zinnii). Many of these cells here terminate distinctly as radial supporting fibres of the retina, presenting either a conical enlargement, or undergoing division; each of the branches again ceasing abruptly like a column upon its pedestal. Other cells intercalated between these reach the surface of the vitreous by a pointed extremity, or break up into fine fibres, so that it appears as though the ends pass into the fibres of the zonula. I have never, however, observed a direct transition of the one into the other. The whole surface of the cells of the pars ciliaris is not unfrequently beset with fine elevations and roughnesses, those of the adjoining cells interlocking with each other. The substance of the cells is not homogeneous, but appears finely striated longitudinally, though not divisible into fibres. Their nucleus is oval, hyaline, relatively large, very pale, like the nuclei of the radial supporting fibres, and is sometimes placed nearer to the one end, and sometimes to the other. Small quantities of dark-brown granular pigment are not unfrequently found in the substance of the cells, which is most closely disposed towards the exterior, so that it is doubtful whether these are peculiar pigment cells (the pigmentary layer of the retina), or whether the pigment cells themselves have not grown out in a fibrous manner. Upon the whole, that view appears to me to be the most correct, according to which the cells of the pars ciliaris correspond to the radial supporting fibres. They agree generally in the nature of their substance, which is in both cases finely striated, and, as it were, fibrillated; in the form and refractive properties of the nucleus; in their relation to perosmic acid, which confers upon both a clear brownish colour, whilst the adjoining vitreous becomes of a

bluish-black colour after long maceration; and lastly, in the rough prickly surface, and the mode of ending at the vitreous.

It is maintained by various authors that the cones of the human retina continuously diminish in number in relation to the rods from the macula lutea to the ora serrata. This, however, is not correct, as I* have already shown. The relative distribution of the rods and cones remains unaltered from a certain line surrounding the yellow spot to the ora serrata, so that three or four rods are always interposed in the direct line between two cones. At the ora serrata the number of the rods suddenly diminishes, and empty spaces occur between the cones. These last, which appear to increase in number, resemble, in a surface view, irregularly circumscribed circles, lose their lustre, and ultimately disappear in the tissue of the pars ciliaris. As was stated by H. Müller, the height of the rods and cones is less near the ora serrata than in the fundus of the eye or near the equator.† Merkel made similar observations in Man, the Ox, Fowl, and Pike.

The condition which Iwanoff and I have named œdema of the retina, associated with atrophy of the nerve tissue at the ora serrata, and to which the latter has recently devoted an extended essay,‡ presents a very remarkable departure from the normal state. According to Merkel § and Iwanoff, it especially occurs in elderly people, consequently may be considered as a senile metamorphosis,|| being characterised by the formation of spaces filled with serous fluid, which, intercommunicating with each other, can detach the retina to a not inconsiderable extent, and lead to atrophy of the nerve tissue at the points in question. The radial supporting fibres, however, become

* *Archiv für Mikroskop. Anatomie*, Band ii., p. 225, Taf. xii., figs. 3, 4.

† See Max Schultze, *Archiv für Mikroskop. Anatomie*, Band v., Taf. xxii., fig. 5, taken from the anterior border; fig. 14, from the neighbourhood of the equator; and fig. 11, from the yellow spot of Man.

‡ Gräfe, *Archiv für Ophthalmologie*, Band xv., Heft. ii., p. 88, 1869.

§ *Macula lutea*, etc., p. 17.

|| Iwanoff, who observed a large number of these cases, saw the œdema in only six amongst fifty eyes of adults between twenty and forty years of age; on the other hand, it was present twenty-six times in forty-eight eyes of adults between fifty and eighty years of age.

compressed into columnar fasciculi, which remain stretched between the two limitantes, or between the limitans interna and the external granulated layer. Though it was originally described by H. Müller* under the impression that the infiltration was a *post-mortem* change, it was first depicted by Blessig,† and first stated to be of frequent occurrence by Henle.‡ When transverse sections of such œdematous spots of the retina are made, cavities are seen in the region of the granule layers, or there may be extensive degeneration of the tissues between the limitans externa and interna, bounded by closely compressed columns of radial fibres, in which are many nuclei, and which form arches near the limiting membranes. Degenerations of this kind, however, are not exclusively limited to the ora serrata. I have myself observed a case where a portion of the retina, the size of a pea, was so infiltrated as to form a prominent tumour near the equator of the eye. Transverse section showed that there was a well-marked state of œdema confined to this spot. The retina was here about one millimeter in thickness. The rods and cones which, in minor degrees of œdema, appear to be unaltered disappear in the more completely distended parts.§ Merkel also observed œdematous swelling of the retina in old Dogs.

6. Development of the Retina.

To form the retina a vesicle is protruded from the brain of the embryo, termed the primitive eye vesicle, which very soon after its appearance becomes changed with coincident development of the lens into a doubly laminated cup. This occurs in Fowls at the end of the second day of incubation. The two laminæ of the primitive retina which originates from the eye vesicle are, in the first instance, of equal thickness; but the anterior lamina, which is in contact with the vitreous, soon

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* *Zeitschrift für wissenschaft. Zoologie*, Band viii., p. 71.

† *De Retinæ structura*, fig. 3, p. 47. Dorpat, 1855.

‡ *Eingeweidelehre*, p. 669.

§ See Iwanoff, *loc. cit.*, Taf. iv. and v., figs. 11 and 12.

increases considerably, whilst the posterior remains unchanged.* The former consists, on the fifth day of incubation, of very numerous small fusiform cells, arranged vertically to the surface; the latter of a single layer of short prismatic cells containing dark pigment. Remak was disposed, in consequence, to recognize in these the first rudiment of the choroid, as well as of the retina. By Kölliker,† however, and more recent inquirers,‡ it has been demonstrated that the development of the pigmented connective tissue and of the vessels of the choroid proceeds independently of the pigmented layer of the primary eye vesicle. The posterior lamina of the latter goes exclusively to form the pigment epithelium of the retina, whilst the anterior lamina forms the remaining layers of this membrane. The rods and cones are the last to appear. Prior to their development the embryonal retina is very sharply defined towards the pigmented epithelium by a limitans externa. This is much more distinct than the limitans interna at the same period of development. It corresponds in regard to its position, lining as it does the cavity of the primary eye vesicle to the inner surface of the cerebral ventricle,§ which in embryoes of the same age I find to be lined by an equally sharply defined membrane. It originates from a conical expansion of fibrils and fusiform cells arranged vertically to the surface, the truncated extremities of which lie in one plane, and are intimately attached to one another to form a membrane. There is thus a complete similarity of structure between the retina and the cerebral ventricles. At this period no epithelial investment exists in either place.

From the seventh to the tenth day of incubation in Chickens,

* See Remak, *Entwickelung der Wirbelthiere*, p. 35, Taf. v., fig 60; Hensen, Virchow's *Archiv*, Band xxx., p. 181; and my detailed account of the development of the retina in the Chick, *Archiv für Mikroskop. Anatomie*, Band ii., p. 239, Taf. viii.

† *Entwickelungsgeschichte der Wirbelthiere*, p. 288, 1861, for Mammals.

‡ Babuchin, *Würzburg nat. Zeitschrift*, Band iv., p. 71, 1863, for Mammals, the Chick, and Frog; Max Schultze in *idem* for the Chick and for Mammals; Schenk, *Sitzungsberichte der Akad. zu Wien*, 1867; April part, for Fishes. See also Hensen, *Archiv für Mikroskop. Anatomie*, Band ii, p. 421.

§ Max Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., p. 265.

a very distinct lamination becomes apparent in what was originally the homogeneous mass of the (anterior) retina. This lamination consists in the differentiation of an internal fibrous layer, of the two granulated layers, and of distinct differences in the size of the cells in the several layers of the granules and ganglion cells; at the same time the rudiments of the rods and cones project posteriorly beyond the membrana limitans externa in the form of homogeneous hemispherical elevations of very small diameter. As these increase in length and thickness the internal segment is first formed, and then subsequently the external segment. These consequently grow into the pigmented epithelial cells of the posterior lamina of the retina, which on their side form the pigment sheaths. On the eighteenth day of incubation, coloured, but at first very small, red and subsequently yellow oil globules appear in the cones, so that the retina of the Chick just escaped from the egg is already provided with completely developed percipient elements, which do indeed increase in length and thickness, but not in number. It is moreover worthy of notice that in Chickens the rods and cones appear from the first as distinct structures, and that the cones, which are originally smaller than the rods, immediately after hatching become considerably thicker, and, with their coloured globules, occupy a much larger space than at an earlier period.

The relation of the developing rods and cones to the external granules has been ascertained by Babuchin from his researches on the retina of the Tadpole.* The large size of the elementary parts permits it to be seen that the rods and cones owe their origin to an outgrowth of the substance of the outer granules, and although when fully developed the rods and cones appear very distinct, the difference, according to Babuchin, in the early stages of development is but slight.

The results of the investigations made by Schenk on Fishes agree well with these observations on the development of the rods and cones from the anterior lamina of the primary eye vesicle. This process, so far as it is connected with the production of cells on one side of a substance differentiated from

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* *Loc. cit.*, p. 77.

protoplasm may be associated with the production of the so-called cuticular formations, at least, so far as regards the outer segments, and the refractile bodies of the internal segments.*

As in Chickens, previous to hatching, the rods and cones are already developed, though they are then of smaller size than in the adult animal, so is it also at the time of birth in Man and in many Mammals, as, for example, in Ruminants. In the new-born Child and in the Calf the rods and cones are well developed, and divided into internal and external segments, though these are much more slender and shorter than in adults. It is different in the blind litters of Cats and Rabbits; here, the percipient elements develop subsequent to birth.† Either at the period of birth the limitans externa is still perfectly smooth, or the first indications of rods and cones begin to project beyond the limiting membrane in the form of rounded elevations; the formation of distinct rod-like elements follows a few days later, and proceeds as in Fowls, so that the internal segment is first formed, and then the external segment. The first distinctly perceptible laminæ of the latter occur at about the fifth or sixth day after birth. At the ninth day, that is to say, at the period when the eyelids open, the length of the external segments in the Cat amounts to scarcely more than four micromillimeters, whilst in the adult animal their length amounts to seventeen micromillimeters. In the Rabbit the proportions are similar.‡ The laminæ consequently increase, not in thickness but in number.§ At what period antecedent

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* Hensen long held the opinion that the rods, or the outer part of their substance, develop coincidently with the pigment from the outer lamina of the primary eye vesicle (Virchow's *Archiv*, Band xxx., p. 181, and *Archiv für Mikroskop. Anatomie*, Band ii., p. 421), but he has lately given up this view (*Ibidem*, Band iv., p. 349).

† Max Schultze, *Archiv für Mikroskop. Anatomie*, Band ii., p. 246, and Band iii., p. 373. Steinlin, *Anatomie der Retina*, St. Gallen, p. 99.

‡ Max Schultze, *loc. cit.*, Band iii., p. 375.

§ For a different view, by W. Krause, see his *Membrana fenestrata*, p. 33. I may here state, that satisfactory conclusions respecting the development of the rods and cones can only be obtained from the borders of folds of absolutely fresh specimens of retinæ, preserved in aqueous humour or iodine of serum, and that *all* my statements rest on the

to birth in Man the development of the rods and cones begins from the outer granule layer has not been accurately ascertained. In an embryo of the twenty-fourth week, which I obtained perfectly fresh, I found the membrana limitans interna still quite smooth. Ritter, however, believes he has seen well-developed rods in younger embryoes.*

In the early stages of its development the retina extends forwards as far as to the border of the lens. In consequence of a difference in the process of development of its several parts, arise the retina proper, its pars ciliaris, and lastly the pigment lying behind the iris, which is covered by only a rudiment of the tissue proceeding from the internal lamina of the primary eye vesicle, which is, it would appear, a variable prolongation of the limitans interna. Inasmuch as during the development of the retina the rudiment of the palpebral fissure of the embryo is indicated by a non-pigmented stria which extends from behind forwards over the whole extent of the retina,† the rudiment of this not unfrequently occasions a persistent absence of pigment as an arrest of development (coloboma), which affects the pigment behind the iris equally with that before the choroid. Coloboma, as Schöler‡ has already demonstrated, is primarily an arrest of development of the retina, and not of the choroid.§ Information as to how far the tissues of the latter membrane and of the iris, apart from the pigment epithelium, take part in the frequently occurring

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examination of such specimens. W. Krause macerates the eyes of young Rabbits in bichromate of potash, and finds that the existence of rods and cones can be demonstrated with extraordinary facility, when I am unable to discover them in the fresh state.

* Gräfe's *Archiv*, Band x., Heft i., p. 75, Heft ii., p. 142. *Die Structur der Retina*, etc., pp. 32 and 52.

† See *Archiv für Mikroskop. Anatomie*, Band ii., Taf. viii., fig 7.

‡ *De oculi evolutione. Dissert. inaugural.* Mitau, 1849.

§ We cannot possibly regard the fovea centralis as a remains of the fœtal palpebral fissure, on account of its position, as Hensen has recently pointed out (*Archiv fur Mikroskop. Anatomie*, Band iv., p. 350). On the other hand, the pecten of Birds, and what corresponds to this in Fishes and Reptiles, are situated in the vicinity of the fissure, whilst they originate from the growth of the choroid into it. Schenk, *Wiener Sitzungsberichte*, 1867.

coloboma, must be obtained from numerous and exact ophthalmoscopic examinations of cases in which this arrest of development has occurred. Here also there are relations in respect to the development of the pigment epithelium from the external lamina of the primary eye vesicle to the development of the choroidal tissue that are quite unknown.

II.

TUNICA VASCULOSA.

By PROF. A. IWANOFF.

The tunica vasculosa, or tunica uvea, lines the sclerotic, and lies between it and the retina. At a distance of one millimeter from the margin of the cornea it makes a sharp curve inwards towards the axis of the eye, and rests on the anterior surface of the lens, forming by means of this rectangularly bent part the posterior wall of the anterior chamber of the eye.

The posterior part of the tunica vasculosa, lining the sclerotic, is termed the choroid; whilst the anterior part, which appears during life behind the transparent cornea, is named the iris, and is perforated at its centre by an opening, the pupil.

These two membranes are together named the tunica vasculosa, because both are richly supplied with vessels, and because both sets of vessels freely intercommunicate with one another. The other term common to the choroid and iris, of tunica uvea, was conferred upon them from their remote resemblance to the skin of a dark-coloured grape, in which the hole for the pedicle corresponds to the pupil.* Many anatomists now limit the term uvea to the layer of pigment that lines the posterior surface of the iris.

I. The *choroid* forms a thin vascular membrane, having a thickness of 0·08 to 0·16 of a millimeter, which is firmly attached to the sclerotic in two places, posteriorly at the point of entrance of the optic nerve, where its inner layers are continuous with a ring that embraces the nerve, and from which fine fibres are given off that penetrate the nerve itself;†

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* Brücke, *Anatomische Beschreibung des menschlichen Augapfels*, p. 2, 1847.

† H. Müller, *Anatomische Beiträge zur Ophthalmologie*, *Archiv für Ophthalmologie*, Band ii., Abtheilung ii., p. 24.

and anteriorly at the point of transition of the sclerotic into the cornea (annular tendon of the circular muscle). These two coats are elsewhere connected by arteries and nerves, which perforate the sclerotic in order to enter the choroid, and by veins which pass in the opposite direction.

The external surface, which is turned towards the sclerotica, is of fibrous structure, and brownish colour; where the choroid is attached in front to the sclerotica, there is an annular grey thickening, having a breadth of from three to four millimeters, which encircles the anterior part of the vascular membrane, and is termed the ciliary muscle.

The internal surface of the choroid looks towards the retina, and is very loosely connected with it as far as the ora serrata, though sufficiently firmly to cause the whole external layer of the retina (namely, the pigmented epithelial layer) to remain adherent to it in the greater number of cases, which has led to the belief that this layer belongs to the choroid. Starting from the ora serrata, these membranes are much more intimately united, since from this point forwards the pigmentary layer, forming a bond of union between the ciliary portion of the retina and the choroid, increases considerably; on which account also the separation of the retina from the choroid at this spot does not always, and then only partially, take place. If the pigment be removed, the inner surface of the choroid, as far as to the ora serrata, appears perfectly smooth, and of a grey colour; behind the ora serrata its surface becomes rough, and in front of it is a series of folds, arranged in a meridianal direction, and separated from one another by deep furrows, which are the so-called ciliary processes.

The *ciliary processes*, from seventy to eighty in number, have the aspect of a regularly plaited frill, and as they project more and more anteriorly their apices ultimately reach the ciliary border of the iris. The entire internal surface and all the folds as far as their anterior margin, are covered with a thick layer of pigment and with the cells of the ciliary portion of the retina (pars ciliaris retinæ).

The anterior part of the choroid, commencing from the ora serrata, together with the ciliary processes and the ciliary muscle, are collectively termed the corpus ciliare.

The anterior part of the choroid has long had a special name applied to it. Thus, Vesalius named it the tunica ciliaris, and subsequent anatomists distinguished in this tunica ciliaris a pars plicata and a pars non plicata. Fallopius was, however, the first who applied the term corpus ciliare to this part of the choroid. Henle only names the most anterior part of the choroid the corpus ciliare, including under this term the ciliary processes and the ciliary muscle. The zone lying between the ora serrata and the corpus ciliare he terms the orbiculus ciliaris, without maintaining, however, that any well-defined line can be drawn between the corpus ciliare and the orbiculus ciliaris. Under the name corona ciliaris, Luschka describes that portion of the membrane which is connected with the zonula Zinnii, and extends from the ora serrata to beyond the margin of the lens; the ciliary muscle he names the annulus ciliaris. We believe that it would be of advantage in facilitating the comprehension of the ordinary terminology to keep to one system of nomenclature, even if this did not express all the anatomical peculiarities of this part of the choroid. We have selected the term corpus ciliare, not because we consider it to be the best, but because it is most generally employed; in this sense Kölliker uses the term corpus ciliare in his Manual, as well as H. Müller in all his treatises on the eye.

The *vessels* form the chief constituent of the choroid, and on this account this membrane has from a remote period been considered to exert a powerful influence on the nutrition of the eye. Its rich supply of vessels explains also, without doubt, the very important part it plays in the various pathological processes taking place within this organ.

The *smooth muscles* form another constituent of this membrane, playing an important part in the functions of the eye. The larger part of them is accumulated in the corpus ciliare, but they are by no means altogether absent in the posterior segment of the choroid.

Lastly, the choroid is abundantly supplied with *nerves*.

All these constituents are connected together by a *stroma*, characterized by the presence of a large number of stellate pigment cells.

The five following layers are usually distinguished in the choroid—the pigment layer; the vitreous layer; the membrana chorio-capillaris; the layer formed by the larger arteries and veins; and lastly, the membrana supra-chorioidea. The history

of the development of the pigment layer from the external lamella of the secondary eye vesicle, shows, however, that it must be reckoned as belonging to the retina; so that there only remain four layers. But inasmuch as this division of the choroid into four layers is not based on any facts of structure or position, we shall not adhere to it in the following account.

1. Vitreous membrane (Glashaut), (lamina vitrea of F. Arnold,* elastic layer of Kölliker,† basal membrane of Henle,‡) was originally described by Bruch,§ by whom it was named membrana pigmenti. In the posterior segment of the choroid it forms a very thin (0·0006—0·0008 of a millimeter) structureless, or slightly fibrous (Kölliker) membrane, which, except by the application of artificial means, is indissolubly connected with the stroma of the choroid. The surface in contact with the pigmented epithelium is perfectly smooth as far as to the ora serrata. Solutions of potash and of sulphuric acid bring its folds into view, because these reagents act differently on the vitreous layer and the external layers of the choroid connected with it. For since the protracted action of these reagents causes a part of the stroma attached to the vitreous membrane to break down; so also, in concentrated acids and alkalies, it frequently separates from the other layers of the choroid in the form of isolated shreds. If the choroid be macerated for some time in a ten-per-cent. solution of common salt, the fibrous structure of the vitreous layer is very clearly brought into view. Even then, however, it presents no trace of nuclei. The nuclei described as existing in it by Bruch and Henle unquestionably belong to the capillaries.

In the anterior portion of the choroid—the corpus ciliare—the characters of the vitreous layer undergo a marked change. It here becomes paler, thicker, and is more amenable to the action of alkalies and acids. It here also loses its smoothness, its inner surface presenting microscopical elevations and de-

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* *Anatomie*, Band ii., p. 1020.

† *Handbuch der Gewebelehre*, p. 661, 1867.

‡ *Handbuch der Systematischen Anatomie des Menschen*, Band ii., p. 620, 1866.

§ *Körniges pigment*, 1844.

pressions, which form the so-called reticulum of the ciliary body.* This reticulum is produced by small elevations anastomosing with one another, and enclosing depressions which contain pigment. The meshes of this reticulum are smaller in proportion to their distance from the ora serrata. The plexiform character of the vitreous layer is preserved as far as to the iris.

2. The vessels of the choroid, as has been already stated, form two layers: the chorio-capillary layer, known also as the membrana Ruyschiana, which reaches only as far as to the ora serrata, and the layer composed of the larger arterial and venous trunks, which has also been termed the tunica vasculosa Halleri. The ramification of these vessels will be hereafter separately described, but a few remarks may here be made in respect to some peculiarities of their structure.

The capillaries are so intimately connected with the vitreous membrane by means of a very thin connective-tissue stroma, that their separation can only be effected by the application of reagents which dissolve the stroma.

The walls of the capillaries present no points of difference in their structure from the capillaries of other regions of the human body. Contrary to the opinion of Henle, their walls contain nuclei; and this not only in young persons, as H. Müller admits, but also in those of advanced age. In old persons, however, the nuclei are somewhat atrophied, become flattened, whilst at the same time the vascular walls are thickened, rendering their observation more difficult.

In many instances we see in the eyes of persons apparently in perfect health elongated cells placed by the side of the capillary wall, from which extremely delicate processes, visible only under the highest powers, extend to the wall; but these cells and their processes, which join to form a plexus, are brought very clearly into view in inflammation of the choroid. In such cases these processes extend themselves also into the interspaces of the capillaries.

The arteriæ ciliares breves are characterized by the great development of their circular muscles. They are accompanied

* H. Müller, *Archiv für Ophthalmologie*, Band ii., Heft ii., *Anatomische Beiträge zur Ophthalmologie*.

on either side by a longitudinal fasciculus of smooth muscular fibres, the size of which varies considerably in different instances.* Moreover, the thickness of the muscular fasciculus is not alike on the two sides of the vessel. The smooth muscles only accompany the short ciliary arteries as far as to the posterior portion of the choroid; the farther they are traced forward in the direction of the ora serrata, the fewer are the muscles.

Detached muscles in the form of thin fasciculi are found also distributed in the stroma of the choroid.

3. The principal mass of the smooth muscular fibres of the choroid is imbedded in the most anterior part of this membrane, and constitutes the *ciliary muscle* (tensor choroideæ, Brücke).

The ciliary muscle (fig. 362) resembles a prism, bent into the form of a circle, with its sharp border turned backwards.

Fig. 362.

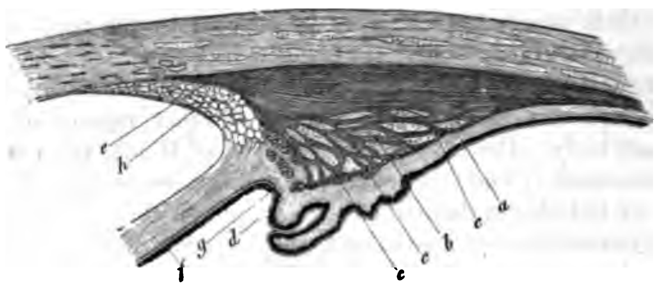

Fig. 362. Section of the ciliary region of the eye of Man. *a*, Meridianal muscular fasciculus of the musculus ciliaris ; *b*, deeper-seated radiating fasciculi ; *c c c*, annular plexus ; *d*, annular muscle of Müller ; *f*, muscular lamina on the posterior surface of the iris ; *g*, muscular plexus at the ciliary border of the iris ; *e*,. annular tendon of the musculus ciliaris ; *h*, ligamentum pectinatum.

Its position is in the anterior and external part of the ciliary body. The ciliary muscle is separated from the sclerotic by a thin layer, the lamina fusca ; and from the pigment which covers the surface of the ciliary processes, by connective tissue.

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* H. Müller, *Verhandlung. der physikalisch-medicinischen Gesellschaft in Würzburg*, Band x., Abtheil. ii., iii., p. 179.

In meridianal sections the ciliary muscle exhibits the form of a rectangular triangle, the shortest side of which is turned forwards, and forms a right angle with the outer side. The thickness of the muscle is about 0·8 of a millimeter.

The greater part of the muscle is composed of meridianally running fasciculi (fig. 362, *a*), forming a compact mass, which constitutes the thick external portion, and makes up its larger third.

The deeper-lying fasciculi (*b*), which, like the preceding, arise at the anterior external angle of the muscle, run divergingly in a radiating manner to the inner side of the triangle. In this course the radiating fasciculi frequently anastomose with one another; after they have reached the inner side they become circular, and thus form a thick circular web along the whole internal muscular surface (*c*).

Moreover, the anterior side, and, to a certain extent, the internal anterior angle of the ciliary muscle, include tolerably thick fasciculi of circular fibres, the so-called *circular or annular muscle of Müller* (*d*). The posterior fasciculi are formed of those longitudinal fibres which have changed their direction, the anterior represent a completely independent muscle.

All the meridianal and radiating fasciculi arise from the anterior external angle of the muscle, and they are continuous with a dense flattened expansion of connective tissue which forms its annular tendon (*e*). This is directed forwards, lies on the inner side of the canal of Schlemm, and is ultimately itself continuous with the tissue of the cornea.

That meridianal portion of the muscle which is in immediate contact with the sclerotic consists anteriorly of regularly arranged parallel laminæ. In proportion, however, as we pass farther backwards, this regularity of disposition disappears, so that at a distance of three millimeters from the origin of the muscle the fasciculi separating and anastomosing with one another, form a series of loops, with their convexities turned backwards, in which a part of the muscle terminates. The other portion of the meridianally running fibrils preserves its primary direction, and may be followed to a distance of from five to six millimeters from the origin of the muscle, in the

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form of extremely fine fasciculi, which are lost amongst the pigment cells in the stroma of the ciliary body.

The further course of these fasciculi can only be followed on the temporal and nasal sides of the choroid, where, united into two fasciculi, they lie on either side of the long ciliary arteries.

H. Müller observed that in many eyes these fasciculi not only accompany the ciliary arteries throughout their whole length, but also accompany them for some distance in the scleral canal.

Fig. 363.

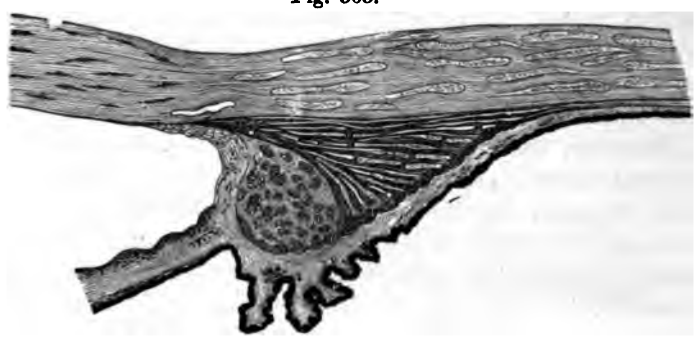

Fig. 363. Section of the ciliary region of a hypermetropic (long or far-sighted) eye.

The ciliary muscle was discovered in 1846, by Brücke,* and soon after, independently, by Todd and Bowman. Brücke and Todd and Bowman only described the meridianal fasciculi.

The most complete description of the muscle was given by H. Müller,† in the year 1857. In this essay he first described the circular fasciculi running parallel to the border of the cornea, which constitute the anterior and inner portion of the ciliary muscle; and were termed by him the compressor lentis. Coincidently Arlt‡ also discovered the circular fibres of this muscle, and described them as being only processes of the radiating fibres.

Finally, in the year 1867, F. E. Schulze discovered, with the aid of

* Müller's *Archiv*, 1846.

† *Archiv für Ophthalmologie*, Band iii.

‡ *Archiv für Mikroskop. Anatomie*, Band iii., p. 477.

chloride of palladium, the annular plexus which is expanded over the whole internal side of this muscle.

The size of the muscle, its texture, and the relative development of its meridianal and circular fibres, are subject to considerable individual variations. These variations are in immediate relation to the length of the optic axis, on which the refraction of the eye, that is to say, its long or short-sightedness, depends.

In hypermetropic persons,* whose optic axis is generally short, the anterior part of the muscle, that is to say, Müller's annular muscle, is relatively largely developed; in consequence of which the muscle projects anteriorly in the direction of the anterior chambers of the eye, and is upon the whole of smaller size.

Fig. 364.

Fig. 364. Section from the ciliary region of a myopic (short-sighted) eye.

In myopics (whose optic axis is considerably longer) the anterior circular muscular fasciculi are very feebly developed; the muscle itself consists chiefly of meridianal and radiating fasciculi, and the anterior part of the muscle consequently appears to be displaced backwards to a considerable extent; and the whole muscle is longer.

In the domestic animals the muscle consists exclusively of longitudinal fasciculi. In the Pig, however, circular fasciculi are found in the posterior part.†

4. The *nerves* of the choroid (nervi ciliares) belong to the third and fifth pairs, and to the sympathetic. The long set,

* A. Iwanoff, *Beiträge zur Anatomie des Ciliarmuskels in the Archiv für Ophthalmologie*, Band xv., Abtheil iii., p. 284.

† A. Iwanoff and A. Rollett, *Archiv für Ophthalmologie*, Band xv., Abtheil i.

(nervi ciliares longi) two, or more rarely three in number, proceed from the ramus naso-ciliaris trigemini; the short set (nervi ciliares breves), fourteen to eighteen in number, proceed from the ganglion ciliare. Both sets perforate the sclerotic near the entrance of the optic nerve, and having gained the interior of the eye, run upon the external surface of the choroid. After they have given off a considerable number of branches to the posterior portion of the membrane, they pass forward to the ciliary muscle, on which, dividing dichotomously, they form a close plexus. H. Müller* found ganglion cells in the angles of the first divisions of these nerves, with a diameter of 0·0016—0·025 of a millimeter, and containing two or three nuclei. In the deep layers of this plexus, lying in the interior of the muscle, we find, in addition, nodal swellings, closely resembling bipolar cells.

The peculiarity of the structure of the nerve plexus in the posterior portion of the choroid is, that the ciliary nerves, immediately after their exit from the sclerotic, and as they run forwards to the ciliary muscle, give off lateral branches, which are composed partly of dark-edged and partly of pale nerve fibres. These lateral branches, after repeated divisions and anastomoses, form a plexus lying between the vessels and the sclerotic. From this plexus delicate filaments may be traced to the arteries, in the smooth muscular fibres of which they appear to terminate. Ganglion cells are also found in this plexus occupying the points of intersection. True ganglia likewise occur in the trunks of the ciliary nerves.

It is worthy of note that both the development of the posterior nerve-plexus, as well as the number of ganglion cells to be met with in this part, undergoes considerable individual variation, and it is also to be remarked that these variations stand in close relation to the development of the smooth muscular fibres in the posterior portion of the choroid.

5. The stroma of the choroid is formed of a close plexus of branched fibres, in the interspaces of which, especially of the outer layers, considerable numbers of stellate pigment cells are imbedded.

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* *Verhandlungen der phys. med. Gesellschaft in Würzburg*, **Band x., p. 108.**

The fibres of this plexus, anastomosing with each other, run for the most part in a direction parallel to the surface of the sclerotic, giving off at the same time but few processes into the adjoining layers; it thus appears as if the fibres were interwoven into several distinct membranes, of which one, the lamina fusca of authors, usually adheres to the sclerotic, and the other thicker one to the choroid. The latter again splits into several superimposed laminæ, which, commencing at the posterior part of the ciliary body, extend to the entrance of the optic nerve (membrana suprachoroidea).

The fibrillar stroma which occupies the interspaces between the vessels is in immediate relation with this membrana suprachoroidea.

The stroma of the choroid contains numerous cells; the most characteristic of these are the stellate pigment cells, which differ somewhat in their form in the superficial and deep layers of the membrane. The cells in the superficial layers are stellate, with short, broad, and flat surfaces; their dark-brown pigment is absent in the immediate vicinity of the nucleus, which is consequently always sharply defined. The deep-lying stellate cells, which completely fill the interspaces between the vessels, are thicker than they are broad, and are provided with long thin processes, which frequently anastomose and form a close plexus with the processes of the adjoining cells. These cells are usually of darker colour than the superficial ones.

Besides pigmented cells, we also meet with the most diverse forms of non-pigmented cells in the choroid. Amongst these the spheroidal cells deserve special notice, which in size and form closely resemble the white blood or the lymph corpuscles.* These are met with in all the layers of the choroid, but chiefly in the deepest layers between the capillaries. Like the white blood corpuscles, they can change their form, and move from place to place. They vary considerably in number, according to age and the healthy state or otherwise of the eye. They are very numerous in children, but are met with in disproportionately small number in adults, in whom, however, their

* Hasse, *Archiv für Ophthalmologie*, Band iv., p. 57.

number varies to a considerable extent. They are abundant in certain intraocular pathological conditions.

The external surface of the suprachoroid coat, according to the recent researches of Schwalbe, is covered with an endothelium.

The question of the nature and kind of tissue of which the choroid is composed cannot be determined exclusively on histological grounds, but requires also an histogenetic investigation. The defective character of the latter has led some to classify the stroma of the choroid with connective tissue, and others with elastic tissue.

II. THE IRIS.—In the iris we distinguish the pupillary border, margo pupillaris, bounding the central opening or pupil; and the ciliary border, margo ciliaris, by which it is attached to the ciliary body and the cornea. It has also an anterior and a posterior surface.

On the anterior surface of the iris is a dentated ridge which divides it into two zones: the internal or pupillary zone, about one millimeter broad, is beset with radiating folds in close apposition to each other; the external or ciliary zone has a breadth of about three millimeters (with an average diameter of the pupil of four millimeters in the dead body), and presents in its peripheric half from five to seven concentrically arranged folds, which always—but especially when the pupil is dilated—project sharply defined.

The anterior surface of the iris is covered by an epithelium, which is really the continuation of the epithelium of the membrane of Descemet, but differs somewhat from this in being composed of smaller cells which are granular, not quite so distinctly hexagonal, and not so sharply differentiated from one another.

The posterior surface of the iris is black, consequent on the presence of a thick layer of pigment. This is the uvea of authors. The uvea begins at the margin of the pupil, which when contracted is distinctly bordered by it (whilst when dilated it vanishes entirely), and terminates at the ciliary border, where it becomes continuous with the pigmentary layer of the ciliary processes. The contour line between these two pig-

ments is always well defined, since that of the ciliary processes is provided, as far as to its point of contact with the uvea, with a layer of the ciliary portion of the retina.

Histologically the uvea is composed of cells, the protoplasm of which is infiltrated with pigment granules, which completely conceal the nucleus. In specimens teazed out with needles, clumps with rough surfaces, and of the most various size, are commonly met with under the microscope. It is impossible from these fragments to determine the form of the cells. The nuclei, when completely freed from pigment, are spheroidal and slightly granular.

The free surface of the uvea possesses a series of radiating slightly projecting folds, which extend from the pupillary to the ciliary border in the form of regularly arranged straight lines; their number is from 70 to 80.

In Man there is no investing membrane for this pigment layer. That which was at one time described under the names of the membrana limitans Pacini, Jacobi, pigmenti, is, according to Kölliker, " the coalesced external cell walls of the pigment cells;" according to Henle, it is the border of the cementing substance which holds the pigment granules together, a view which appears so much the more probable, as no walls can be perceived in the cells of these layers.

The tissue of the iris, like that of the choroid, is composed of vessels, muscles, nerves, and stroma.

The *vessels* of the iris are characterized, speaking generally, by the extraordinary thickness of their walls (Arnold), and especially of their adventitia (Henle), which is considerably thicker than all the rest of their coats put together. The musculature of the vascular walls is also remarkably developed (Arnold and Hüttenbrenner).

The movements of the iris are effected by means of two muscles,—the sphincter, by which the pupil is contracted, and the dilatator, by which it is enlarged.

The sphincter of the pupil (fig. 365, *a*) occupies the pupillary zone of the iris, and extends outwards to a distance of from 0·9—1·3 millimeters. At the pupillary border it is thin (having a thickness of 0·10 of a millimeter); but further outwards it becomes thicker, and not far from its external margin it attains

a thickness of 0·25 of a millimeter. It is situated towards the posterior surface of the iris, and is separated from the uvea only by a thin layer of connective tissue, and some extremely delicate muscular fasciculi belonging to the dilatator.

The dilatator pupillæ (fig. 365, *b*) is developed from the fasciculi of the sphincter, of which it constitutes the unbroken continuation. It commences in a series of arcuate interwoven fasciculi that are partly situated in the interior of the sphincter, and partly lie on its posterior surface, between it and the pigment layer. These several fasciculi, after they have passed beyond the boundary of the sphincter, unite to form a continuous muscular lamina, extending over the whole posterior surface of the iris (fig. 362, *f*), all the fibres of which lie parallel to one another, and are all directed radially from the pupillary to the ciliary border.

Fig. 365.

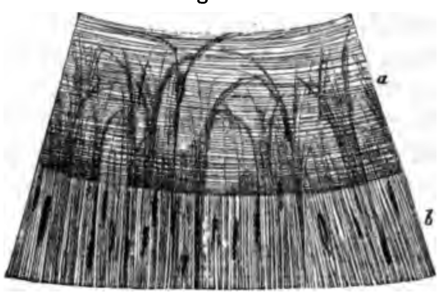

Fig. 365. Segment of the iris, seen from the surface. *a*, Sphincter; *b*, dilatator.

At a distance of half a millimeter from its insertion, the muscle breaks up into separate fasciculi, which are arranged in two layers, one lying upon the other (fig. 366, *a a*). The fibres of these fasciculi having arrived at the ciliary border, immediately change their direction, curve round (*b*), and form by their interlacement a thin muscular plexus (*c*), which runs circularly round the ciliary border of the iris (fig. 362, *g*).

The literary history of the dilatator pupillæ leads us irresistibly to the conclusion that, up to the time of Henle, the existence of this muscle in *Man* was admitted rather in obedience to urgent physiological requirements than from its having been actually demonstrated. That it

had been seen in animals by the greater number of authors is indisputable, and it is equally probable that they then transferred the results of their observations directly to Man, yet this is certainly not feasible on the ground of the peculiarities which the whole arrangement of the accommodation and the muscular mechanism exhibit in Man. The peculiarities in the structure of the dilatator in Man compel Henle himself to make the correct statement that no agreement exists between the object of his description, and that which has been described as the dilatator by Brücke and Henle.

Kölliker* does not attempt to conceal the fact that his account is taken from that of the dilatator of the Rabbit. According to him, the dilatator consists of several thin fasciculi which lie between the vessels, and

Fig. 366.

Fig. 366. Disposition of the muscular fasciculi of the iris. The lettering explained in the text.

consequently in the substance of the iris. Henle† refers to a special layer of fibres which he finds on the internal surface of the iris, and is of opinion that in this homogeneous and continuous, though very thin, layer of radial fibres extending from the pupillary to the ciliary border he has discovered the muscle, the contraction of which effects the dilatation of the pupil.

This statement led to further researches upon the dilatator. According to Hüttenbrenner,‡ the dilatator in Rabbits is formed by the continuous layer of muscular fibres described by Henle, lying immediately behind the epithelium, which in that animal represents the

* *Handbuch der Gewebelehre des Menschen*, 1867, § 667.

† *Handbuch der systematischen Anatomie des Menschen*, Band ii., p. 635.

‡ *Sitzungsberichte d. K. Akademie der Wissenschaften zu Wien*, Abtheilung i., 1868.

pigment layer. This muscle extends to the ciliary border, and some of its fibres can easily be followed as far as to the ligamentum pectinatum. It is obvious that this is not the muscle seen in Rabbits by Kölliker. In Hüttenbrenner's opinion, the dilatator in Man is similarly disposed. Thus it appears that this author, with the single exception of the passage of muscular fibres into the ligamentum pectinatum, corroborates the views of Henle, not only in the case of Man, but in that of animals.

The account of the dilatator given by Merkel,* on the other hand, is more in accordance with Kölliker's definition; he does not describe a continuous layer unbroken by perforations, such as Henle saw, but a number of isolated fasciculi, which however, as Henle states, are placed immediately behind the pigment.

Dogiel† described a muscle which answers to the descriptions given by Brücke and Kölliker; it commences at the sphincter, on the anterior surface of the iris; then, divided into separate fasciculi, runs outwards between the vessels, and is attached to the ciliary ring.

In view of these conflicting statements, I suggested to Herr Jeropheeff to examine the dilatator in Man. The results of his investigation are given above, and are in complete accordance with Henle's description. Herr Jeropheef has also been successful in discovering circular fasciculi at the ciliary border.

The *nerves* of the human iris, in consequence of the great difficulties that oppose themselves to their investigation, have as yet been very unsatisfactorily examined. The best account is that given by Arnold,‡ which, however, treats only of the nerves of the Rabbit.

The nerves of the iris are branches of the ciliary nerves of the choroid. On reaching the iris, they divide dichotomously in its external parts; form arches, and then break up into a plexus consisting of medium-sized branches of nerves. In this plexus an interchange of fibres takes place between the nerve-trunks, which strongly resembles the grouping of the fibres in the chiasma nervorum opticorum.

Three kinds of nerve fibrils proceed from these points of

* *Zeitschrift für rat. Medicin*, Bande xxxi. and xxxiv.

† *Archiv für Mikroskopische Anatomie*, Band vi., p. 95.

‡ *Archiv für pathol. Anatomie und Physiologie*, Band xxvii., *Ueber die Nerven und das Epithel der Iris.*

decussation: *a*. Pale fibres, in all probability belonging to the sympathetic, which run towards the posterior surface of the iris (consequently to the dilatator), on which they form a very fine plexus. *b*. Medullated fibres, which pass to the anterior surface, and there break up into a close plexus of fine fibres; these are the sensory fibres of the iris. *c*. Lastly, a third plexus is distributed within the sphincter; its delicate nerves are for the most part motor.

The vessels, muscles, and nerves of the iris are imbedded in a *stroma*, which is chiefly composed of connective-tissue fibrils and cells.

The connective tissue accompanies the vessels in the form of thin fasciculi of fibrils; but fibres are also met with in the interspaces, most of which run in a longitudinal direction.

In black eyes the principal portion of the stroma is composed of pigmented stellate cells, which form close anastomoses with each other. These cells are most closely arranged in the most superficial layers of the iris. In black eyes we meet also with many free, round, strongly pigmented cells.

In light-coloured eyes, non-pigmented stellate cells, with long thin processes, are met with, and, in addition, a great number of round cells resembling the lymph corpuscles.

III.

THE BLOODVESSELS OF THE EYE.

By Th. LEBER.

THE bloodvessels of the globe of the eye form *two* completely separate systems; the *vascular system* of the retina, and the *choroidal* or *ciliary* vascular system, which are only connected with each other by means of a number of small branches at the point of entrance of the optic nerves.

The *vascular system of the retina,* in addition to supplying the retina, supplies also a portion of the trunk of the optic nerve; whilst the *ciliary vascular system,* besides supplying the vascular membrane of the eye (including the choroid, ciliary body, and iris), gives branches also to the sclerotic, the margin of the cornea, and the immediately adjoining portion of the scleral conjunctiva.

The remaining portions of the conjunctiva receive special vessels, which proceed from those of the lids, and form the *conjunctival vascular system.*

1. Vascular System of the Retina.

The vascular system of the retina is formed by the arteria and vena centralis retinæ. The artery is one of the first branches of the ophthalmic artery, and penetrates obliquely into the trunk of the optic nerve, at a distance of fifteen to twenty millimeters from the eye, the vein entering a little nearer to the globe. The latter, as a rule, opens directly into the sinus cavernosus, previously communicating by means of a few large branches with the V. ophthalmica superior, but sometimes opening directly into the latter. More rarely it opens into the

V. ophthalmica inferior.* The arteria and vena centralis retinæ (fig. 367, *e e*) run close to one another in the axis of the optic nerve, surrounded by some connective tissue as far as to the intra-ocular extremity of the nerve. In their course they give off small branches to the trunk of the optic nerve, which run in the plexiform trabeculæ of connective tissue that invest the nerve fasciculi.

In addition to the branches of the central vessels, the optic nerve also receives many twigs from the vessels supplying the internal sheath, *f*, (or proper neurilemma of the nerve,) and, though in smaller number, from those of the external sheath, *g*. These vessels are branches of the ophthalmic artery, and of its primary divisions. The intra-cranial portion of the optic nerves, the chiasma and the tractus opticus, are supplied by the vessels running in the adjoining parts of the pia mater and brain, the branches of which communicate with those of the intra-orbital part of the nerve.

At its point of entrance into the eye, the optic nerve receives also branches from a few (two or three) of the posterior short ciliary arteries, *k*. These form a complete vascular circle, named the *circle of Zinn or Haller*,* which gives off numerous fine branches into the optic nerves, that anastomose with the branches of the central artery.

Veins corresponding to these branches of the ciliary arteries, there are none; on the other hand, the small arteries, veins, and capillaries of the choroid communicate directly at the margin of the optic disk with the corresponding vessels of the papilla and of the external sheath of the optic nerve, so that a tolerably ultimate connection is here established between the retinal and ciliary vascular systems, *l*. No other communication exists between the two. At the ora serrata the vascular system of the retina ceases with the formation of capillary loops, without communicating at any point with that of the choroid.

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* Waller, *De venis oculi*, Berol, 1778. Sesemann, *Die Orbitalvenen des Menschen und ihr Zusammenhang mit den oberflächlichen Venen des Kopfes* (The orbital veins of Man and their communications with the superficial veins of the head), in Reichert and Dubois-Reymond's *Archiv*, 1869, p. 2.

* Illustrations of which will be found in *Jäger ueber die Einstellungen des dioptric. Apparats*, Taf iii., figs. 34—36 (Wien, 1861); and Th. Leber, *Denkschrift. d. Wien. Akad.*, Band xxiv., Taf. iv.

Fig. 367.

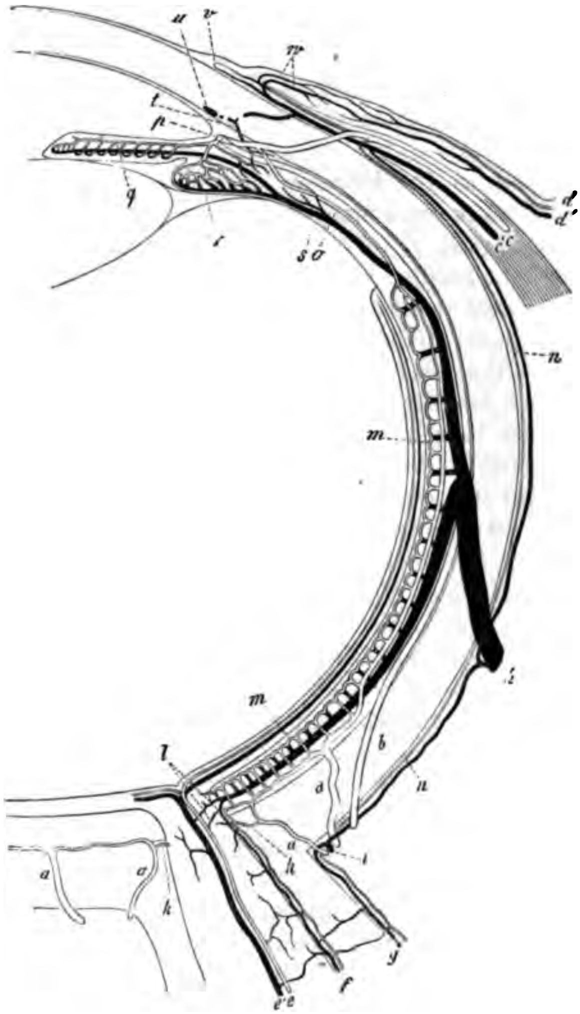

Fig. 367. Diagrammatic representation of the course of the vessels in the eye; horizontal section; the veins represented black, the arteries clear. *a*, Arteriæ ciliares posteriores breves; *b*, arteriæ ciliares posteriores longæ; *c'c*, arteriæ et venæ ciliares anteriores; *d d'*, art. et ven. conj. posteriores; *e'e*, arteriæ et ven. centrales retinæ; *f*, vessels of the internal, and *g*, of the external optic sheath; *h*, vena

The arteria and vena centralis run in the axis of the optic nerve, to the surface of the papilla, at which point, or somewhat earlier, they break up into their principal branches, the vein usually dividing somewhat earlier than the artery. The mode of branching is dichotomous. A main branch, both of the artery and vein, runs upwards; the others downwards, and these again quickly subdivide and diverge at different angles from one another. The veins pursue approximatively the same direction as the arteries, at least in their larger branches, and are usually of larger size. Numerous variations, within certain limits, occur in different individuals. No large vessel ever runs outwards towards the temple, and over the macula lutea, except in extremely rare cases (Mauthner); all the larger vessels curve round the yellow spot, to reach the peripheric portions of the retina, and send small branches from all sides into the macula. Similar small vessels pass to it also directly from the papilla. These supply the macula, but all terminate at the border of the fovea centralis by means of capillary loops, so that this last is quite destitute of vessels.

The capillary plexus of the retina is distinguished from that of the choroid by its much wider meshes, the capillaries themselves are finer and very thin-walled. The mode of ramification of the retinal vessels closely resembles that of the central organs of the nervous system. According to His, perivascular lymph spaces surround the retinal vessels very similar to those of the vessels of the brain and spinal cord.

The larger branches of the central vessels all run in the nerve-fibre layer of the retina, and become smaller in proportion as they are situated more externally in the successive layers of the retina. The smaller branches penetrate as far as

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vorticosa; *i*, venæ ciliares posteriores breves; *k*, branch of the art. cil. post. brev. to the optic nerve; *l*, anastomoses of the choroidal vessels with those of the optic nerve; *m*, chorio-capillaris; *n*, episcleral branches; *o*, arteria recurrens choroidalis; *p*, circulus arteriosus iridis major (transverse section); *q*, vessels of the iris; *r*, of the ciliary process; *s*, branch to the vena vorticalis from the ciliary muscle; *t*, branch to the anterior ciliary vein, proceeding from the ciliary muscle; *u*, circulus venosus; *v*, marginal loop-plexus of the cornea; *w*, arteria et vena conjunctivalis anterior.

to the intergranule layer; the external granule layer and the bacillar layer are, like the fovea centralis, destitute of vessels.

In the fœtus the central artery gives off the arteria hyaloidea, which runs forwards from the papilla, through a canal in the vitreous, to the posterior surface of the lens which it covers with vessels. In the new-born child it is already completely atrophied, the artery being very rarely visible after birth, and even then being generally in an obliterated state.

In many animals the retinal vessels are absent, or are only distributed to a definite portion of the retina.

In Birds, many Amphibia, and Fishes, they are altogether absent; but are here for the most part, though not always, replaced by the vessels of the hyaloidea, which are distributed to the inner surface of the retina (Huschke, Hyrtl, H. Müller). Amongst Mammals, the Rabbit possesses vessels only in that portion of the retina characterized by the presence of medullated nerve-fibres. In the Horse there are only very small vessels, which break up to form a circle of capillary loops not more than from three to six millimeters in diameter.* In the Guinea-pig, very fine vessels are occasionally seen on the papilla of the nerve, which, however, cannot be followed upon the retina.

2. Ciliary or Choroidal Vascular System.

The entire choroidal tract, the sclerotic with the margin of the cornea, and the immediately adjoining parts of the scleral conjunctiva, are supplied by the so-called ciliary vessels. They are the following:—

a Arteries.

1. The *short posterior ciliary arteries* (*arteriæ ciliares posteriores breves*, figs. 367 and 368, *a*,) form from four to six small trunklets, that spring from the ophthalmic artery or its first branches. Pursuing the same course as the optic nerve, they divide into a great number of branches (about twenty), which perforate the posterior segment of the sclerotic in a nearly straight direction from without inwards. The most numerous as well as the largest branches occur in the vicinity of the posterior pole of the eye, internal to the entrance of the optic nerve

* H. Müller, *Notiz über die Netzhautgefässe bei manchem Thieren* (Observations on the retinal vascular system in various animals), *Würzburg Naturwissenschaft. Zeitschrift*, Band ii., p. 64.

and its immediate neighbourhood. The latter are usually of smaller calibre. Some give off the branches already mentioned to the optic-nerve entrance.

Fig. 368.

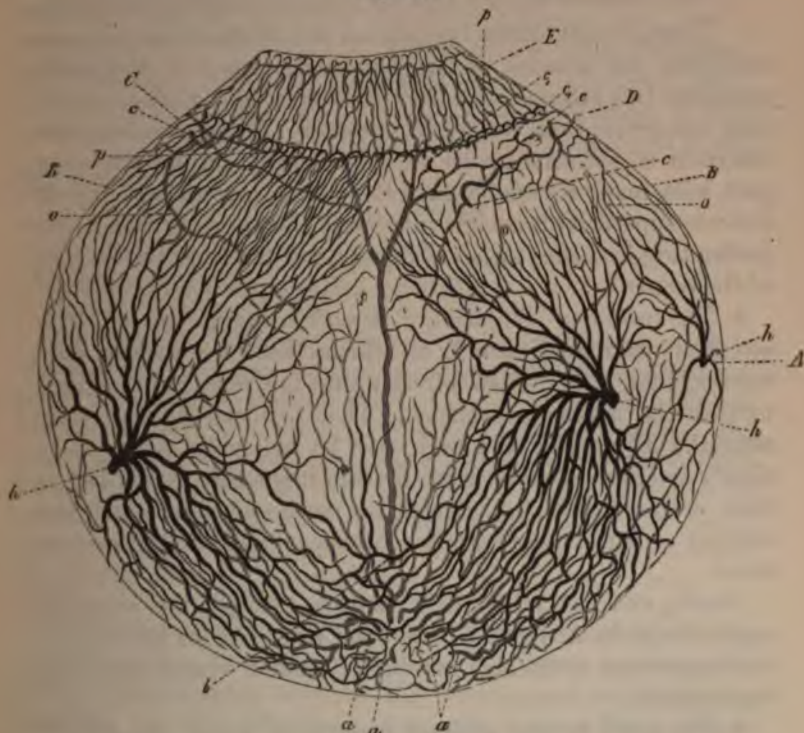

Fig. 368. Semi-diagrammatic representation of the choroidal vessels. *A*, Chorioidea; *B*, pars non-plicata of the ciliary body, orbiculus ciliaris; *C*, ciliary processes (the ciliary muscle is supposed to have been removed); *D*, ciliary muscle; *E*, iris; *a*, arteriæ ciliaris posteriores breves; *b*, arteria ciliaris posterior longa; *c*, arteriæ ciliares anteriores; c_1, venæ ciliares anteriores; *h*, venæ vorticosæ; *o*, arteriæ recurrentis choroideæ; *p*, circulus arteriosus iridis major.

2. The *long posterior ciliary arteries* (*arteriæ ciliares posteriores longæ*, *b*,) have the same origin as the short. They are two in number, and perforate the sclerotic in the horizontal meridian of the eye, somewhat more anteriorly than the latter,

the one on the median, the other on the temporal side. They perforate the sclerotic very obliquely, so that the artery runs in a canal, in the substance of the sclerotic, of as much as four millimeters in length.

3. The *anterior ciliary arteries* (*arteriæ ciliares anteriores*, *c*). These are not direct branches of the ophthalmica, but proceed from the arteries of the four recti muscles. Generally speaking, two arteries arise from each muscle, though as a rule only one comes from the rectus externus. They pass from the insertion of the tendons on to the sclerotic, run for the most part, with many curves, towards the cornea, and after giving off delicate superficial branches, penetrate the sclerotic with their perforating branches rather obliquely, not far from the margin of the cornea.

b. The *veins of the ciliary vascular system* are—1. The so-called *venæ vorticosæ*, *h*, of which there are usually four trunks, that either open directly into the vena ophthalmica, or into the muscular branches. They perforate the sclerotic near the æquator of the bulb, just as obliquely as the long ciliary arteries. One or more of them frequently divide before their entrance into the sclerotic, in consequence of which the number of perforating branches is increased to six, but seldom more.

During and just after their passage through the sclerotic, again, divisions frequently occur; and thus, besides the four or six larger ones, a variable number of smaller vessels pass into the choroid.

2. The small *venulæ ciliares posteriores breves* (fig. 367, *i*), which, like the corresponding arteries, emerge from the sclerotic in the neighbourhood of the optic nerves, but correspond only to the scleral branches of the latter, and receive no branches from the choroid. They are consequently much less numerous and much smaller than the corresponding arteries.

3. The *venæ ciliares anteriores*. These, like the corresponding arteries, are branches of the veins of the recti muscles, but are smaller than the arteries, because the region in which their perforating branches ramify is much more limited in extent.

There are no veins that correspond in their course with posterior long ciliary arteries.

A. The Sclerotic.

This coat receives small branches from all the vessels just described. They are not, however, very numerous, and form a wide-meshed plexus chiefly upon the surface, in which, as a rule, two veins, one on either side of it, accompany each artery. The relations of the episcleral vessels in the anterior segment of the sclerotic, adjoining the margin of the cornea, are different from this, and will receive subsequent consideration in connection with the vessels of the margin of the cornea and of the conjunctiva.

B. The Choroid.

The choroid is supplied by a very large number of vessels, which very freely branch and interweave.

This rich plexus of vessels, which attains its fullest development in the ciliary processes, appears to be destined to secrete the fluid that preserves the intraocular pressure which would otherwise rapidly undergo diminution, owing to filtration through the fibrous capsule. The vessels of the choroid may also, perhaps, be destined for the nutrition of the external non-vascular layers of the retina; and this is rendered so much the more probable by the circumstance mentioned above, that in many animals the whole retina is destitute of vessels, in which case its nutrition must necessarily be maintained by the choroid.

From the preceding enumeration of the vessels of the ciliary vascular system, it is obvious that there is by no means a complete correspondence between the arteries and veins of the choroid. *The choroidal tract in relation to its arterial supply is divisible into two tolerably separate districts; one of which, formed by the choroid proper,* receives its supply from the *short posterior ciliary arteries,* whilst the other, *consisting of the ciliary body and iris,* is supplied by the *long posterior* and the *anterior ciliary arteries.* The most anterior part of the choroid, however, receives in addition a number of recurrent branches from the anterior district, whereby a communication is effected between the latter and the district supplied by the posterior arteries. The efflux of venous blood is differently provided for. The greater part of *the venous blood of the entire choroid* (including the iris and ciliary processes), *has a common outle*

through the venæ vorticosæ, a portion only of the blood of the ciliary muscle discharging itself externally through the small anterior ciliary veins; which portion is far inferior to the other in importance.

(1.) Arteries of the Choroid.

The small trunks of the short ciliary arteries in the posterior segments of the choroid lie at first in the most superficial layers of the membrane, surrounded by a loose, and for the most part darkly pigmented tissue. As they pass forwards they are very tortuous, and, dividing dichotomously, gradually dip into the deeper layers. The finest branches break up into the capillary plexus which covers uniformly the whole internal surface of the choroid, forming the so-called choriocapillaris. The ramifications which run forward are differentiated from the veins by their straighter course, whilst the finer branches found in the neighbourhood of the optic nerves are, like those of the veins, very tortuous. This circumstance, together with the large number of vessels here present, gives the whole membrane the appearance, in well injected specimens, of being an inextricable convolute of minute vessels.

Besides the branches which break up into capillaries, there are no other branches,* as was formerly admitted, which directly discharge themselves into the veins. The belief in the presence of the latter was dependent on illusory appearances, which were easily produced in the methods of opaque injection formerly employed, but which are completely removed by the use of coloured transparent injections.†

The short ciliary arteries break up completely into the capillary plexus of the choroid, and give off no branches for-

* Brücke, *Anatomische Beschreibung des menschlichen Augapfels* (Anatomical description of the Eye of Man), p. 14. Berlin, 1847.

† Th. Leber, *Anatomische Untersuchungen über die Blutgefässe des menschlichen Auge* (Anatomical researches on the bloodvessels of the Eye of Man), *Denkschrift der Akademie zu Wien*, Band xxiv.; *Math. Naturwissensch. Classe*, p. 301; also *Untersuchungen über den Verlauf und Zusammenhang der Gefässe im menschlichen Auge* (Researches on the course and communications of the vessels of the Eye in Man), *Archiv für Ophthalmologie*, Band xi., p. 15.

wards to the ciliary processes and the iris. The admission formerly made of the presence of such branches depends on the veins that pass from the ciliary processes to the venæ vorticosæ having been mistaken for them. On the other hand, the most anterior portion of the choroid receives a number of *recurrent branches** from the ciliary body, which proceed from the long posterior and anterior ciliary arteries. These, varying in number and size, run backwards at considerable distances from each other, between the numerous parallel veins of the orbiculus ciliaris, supplying the most anterior portion of the choroid with capillaries, and also partially anastomosing with the terminal branches of the short posterior ciliary arteries.

The *capillary plexus* forms a uniform layer covering the whole internal surface of the choroid from the optic-nerve entrance to the margin of the orbiculus ciliaris (which corresponds to the ora serrata of the retina), and here terminates with an irregularly dentated margin. Near the optic nerves the meshes are irregularly rounded and very small; but in proportion as they are more distant from the nerve they become more elongated in form, the long diameter ultimately becoming from eight to ten times longer than the short. Moreover, the diameter of the capillaries themselves becomes somewhat greater. There are no true capillaries in the orbiculus ciliaris.

(2.) ARTERIES OF THE CILIARY BODY AND OF THE IRIS.

The two long posterior ciliary arteries, after their passage through the sclerotic, are situated on the external surface of the choroid, and run without dividing horizontally forwards to the ciliary muscle. Here they divide into two branches, which separate at an acute angle, and penetrate into the substance of the muscle, and having reached the anterior border curve round, so that the two branches of each artery together encircle the

* These recurrent branches were first described and depicted by Haller, (*Tabulæ arteriarum oculi*, Tab. vi., fig. 4), and subsequently by Zinn (*Descriptio anatom. ocul. human.* ed. by H. A. Wrisberg, Göttingen, 1780, p. 39), whose account, however, had fallen into oblivion until I redisco- it (*loc. cit.*, pp. 303 and 306, Taf. ii., fig. 12).

globe of the eye. The vascular circle thus formed is completed by branches of the anterior ciliary arteries, which pass directly from the sclerotic to the ciliary muscle. By this means a complete arterial circle is produced at the anterior border of the muscle, termed the *circulus arteriosus iridis major,* which is distributed chiefly to the iris and the ciliary processes, whilst the arteries of the ciliary muscle and the rami recurrentes of the choroid are given off directly to it by the ciliary arteries.

In many animals in which the ciliary processes advance farther upon the posterior surface of the iris, as for example in the Rabbit, the circulus iridis major does not lie in the ciliary muscle, but in the iris at a small distance from the ciliary border.

In addition to the circulus iridis major, the long and anterior ciliary arteries form still further backwards in the ciliary muscle an incomplete circle of anastomoses.

The *arteries of the ciliary muscle* branch in an arborescent manner, and following the direction of the muscular fasciculi, form a tolerably dense trellis-like plexus, which differs in a very marked manner from the plexus of the subjacent ciliary processes.

The *arteries of the ciliary processes* proceed from the circulus iridis major, and must all therefore, like those of the iris, first pass through the ciliary muscle. They are small branches, which quickly break up into a large number of branches that frequently anastomose with each other, and gradually dilating become continuous with the commencement of the veins. Owing to their frequent anastomoses, these capillary veins form a very rich vascular plexus that constitutes the principal portion of the ciliary processes.

The remarkable increase in the extent of surface caused by the numerous larger and smaller lamelliform processes and the intervening channel-like depressions, the great width of the capillary veins, the resulting retardation of the current of the blood, and the thinness of the walls of the vessels, co-operate in rendering the ciliary processes the chief agents for the secretion of the intraocular fluids.

The *arteries of the iris* spring from the anterior border of the circulus arteriosus major, in the form of numerous and

rather tortuous trunklets, which divide dichotomously in the substance of the iris. Their walls are thick in proportion to their calibre. Their ramifications appear upon the anterior surface of the iris as radially running vessels, anastomosing in a plexiform manner, and of the same colour as the iris itself, except in Albinos, in whom the colour of the blood shines through the walls. Not far from the pupillary margin the arteries form a circle of anastomoses, the so-called circulus iridis minor.

The capillary plexus of the iris has much wider meshes than that of the choroid; at the pupillary margin the finest arterial twigs bend round in loops to become continuous with the commencement of the veins. The sphincter pupillæ is traversed by a peculiarly fine capillary plexus.

(3.) Veins of the Choroid.

The *venæ vorticosæ* (*h*), numbering as a rule from four to six large, with frequently a variable number of small vessels (in some instances amounting to as many as ten), are characterized by the whorl-like arrangement of their branches, which radiate outwards in all directions. The smaller vessels form incomplete vortices; receiving vessels from certain directions only. The larger ones, on the other hand, collect their branches from every side, and receive the blood from the choroid proper, the ciliary body, and the iris. Their ramifications form very numerous anastomoses, which, lying on a superficial plane, decussate, for the most part at very acute angles, with the straighter ciliary arteries. Between each two adjoining whorls, loop-like anastomoses wander over the posterior segment of the choroid, which sometimes also receives a number of straighter branches from the fore part. The veins of the iris, of the ciliary processes, and a portion of the veins of the ciliary muscle, form numerous parallel and frequently anastomosing vessels of nearly equal size, which run backwards through the orbiculus ciliaris (pars non-plicata) to the choroid. In the region of the ciliary body they all lie upon the inner surface of the membrane, but pass to the outer surface of the choroid at the ora serrata. They gradually unite to form larger vessels, and having reached the choroid, receive branches from that mem-

brane, and there constitute the anterior branches of the venæ vorticosæ.

These parallel veins of the orbiculus ciliaris, between which, at great distances from each other, the arteriæ recurrentes run, were formerly considered to consist for the most part of arteries, and gave occasion for the admission of the so-called anterior branches of the arteriæ ciliares posteriores breves.

A part only of the veins of the ciliary muscle unite to form the small venæ ciliares ant. (*c*), which perforate the sclerotic near the margin of the cornea, and discharge themselves into the veins of the recti muscles.

These veins communicate with the *venous vascular circle* (*v*), discovered by Schlemm, which is situated in the deepest layers of the sclerotic, close to the corneal margin, and which is usually termed the canalis Schlemmii, circulus or sinus venosus corneæ, and by me the *plexus ciliaris venosus.** This is in reality by no means a simple canal, but a plexiform circle of veins,† which nevertheless presents certain differences in different eyes, and in different parts of the circumference of the same eye. As a rule, it appears in correspondence with the ordinary description as a large (one-fourth of a millimeter wide), flattened, and very thin-walled vein, but is almost always accompanied by one or more small veins, which branch off from it, and after a short course again open into it. At many points the larger vein splits up into two, three, or more correspondingly fine branches, which anastomose, and gradually reunite to form a large vessel. Very frequently the two branches resulting from a division immediately reunite, so that the course of a large vein is as it were interrupted by a small island. Less frequently a large number (from five to seven) of small, frequently anastomosing veins, either running close to one another, or partially overlapping, occur, which then form a delicate plexus, or may gradually again coalesce to form a large vessel.

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* *Loc. cit.*, p. 19. For illustrations see Taf. iii. and the *Archiv für Ophthalmologie*, Band xi., Heft. i., Taf. ii., fig 2.

† Rouget, *Comptes rendus et Mémoires de la Société de Biologie*, 1856, p. 118.

The plexiform character of this vascular circle is not equally well marked in all eyes; it occurs especially in those parts of the circumference where the veins proceeding from the ciliary muscle join it. These pass at the anterior extremity of the muscle to the internal surface of the sclerotic (in one case I counted from twelve to fourteen of them), divide near the venous circle into several anastomosing branches, which partly perforate the sclerotic obliquely, in order to join with the episcleral venous plexus (see below) and the veins of the recti muscles, and partly enter the circulus venosus itself. At these points the latter often appears to be dilated, whilst it is prolonged directly into the plexus of the veins emerging from the ciliary muscle, or forms itself a circular venous plexus.

Moreover in vertical sections made in the region of the margin of the cornea, especially in injected specimens, we almost always find, besides the single large vascular lumen, one or more smaller ones, or we may meet with two or more lumina, which not unfrequently anastomose with each other.

The venous circle of Schlemm appears to constitute a kind of reservoir for the blood of the ciliary muscle in the varying conditions of its contractions. The position of the channel in regard to the muscle is such that the contraction of the latter may occasion a dilatation of the vessels forming it.

In most animals a circular venous plexus occurs at the same point. (Rouget, G. Meyer, Iwanoff, and Rollett.)

In the preceding description I trust I have avoided the objection raised by Henle* to my former account, that I laid too much stress upon the plexiform character of the circulus venosus. I certainly never thought, as Henle appears to believe,† that the circle is always composed of a large number of small vessels. The confounding of the circulus venosus with the so-called canal of Fontana (which is present in the Ox, but not in Man), formerly led to great confusion, which has recently been revived by Pelechin,‡ but the distinction between

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* *Jahresbericht über d. Fortschritte der Anatomie für* 1865, *Zeitschrift für rat. Med.*, Ser. iii., Band xxvii., pp. 96 and 97.

† *Handbuch der Anatomie*, Band iii., Heft i. *(Gefässlehre)*, p. 344, note.

‡ *Ueber den sogenannte Kanal von Fontana oder Schlemm* (On the so-

them was long ago pointed out by Brücke * and Rouget, † and more recently by Iwanoff and Rollett. ‡

An analogous structure to the peculiar trabecular tissue which fills the canal of Fontana, occurs, according to these observers, in Man also, though in small amount; this is the so-called ligamentum pectinatum, that extends from the border of the membrane of Descemet over the circulus venosus, towards the insertion of the ciliary muscle and the origin of the iris.

The circulus venosus may be injected both from the ophthalmic artery and vein, though not readily, without extravasation. § Owing to such extravasations the plexiform structure of the venous circle is more or less concealed, but the extravasations are recognized easily by their having no sharply defined contour. Extravasations are produced still more readily by direct injection through simple penetration with the point of the canula, for which purpose mercury was formerly employed. I have recently found, however, that Prussian blue and glycerine can be thus injected with great facility, and, in part at least, without extravasation, into the vascular circle, and that the fluid penetrates by this means at a low pressure into the finest branches of the episcleral veins, and into those of the ciliary muscle.

These experiments with injection fluids, the presence of blood in the dead body, especially in those who have been hanged (Schlemm), and the demonstration of a thin vascular wall which may be made with facility in transverse sections, may be collectively regarded as finally proving the blood-vascular nature (still doubted by many) of the circulus venosus. ||

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called Canal of Fontana or of Schlemm), in the *Archiv für Ophthalmologie*, Band xiii., Heft ii., p. 425, *et seq.*

* *Anatomische Beschreibung d. menschlichen Augapfels*, pp. 52 and 53.

† *Loc. cit.*, p. 117.

‡ Iwanoff and Rollett, *Bemerkungen zur Anatomie der Irisanheftung* (Remarks on the anatomy of the attachment of the Iris, etc.), *Archiv für Ophthalmologie*, Band xv., Heft i., p. 23, *et seq.*

§ Though Pelechin was not able to effect this, I may adduce my own experience in opposition; for I found, when the injections were otherwise successful, the vessels of the circulus venosus were, as a rule, filled.

|| The essay of Schwalbe on the Lymphatics of the Eye and their limits,

c. The Margin of the Cornea.

At the anterior part of the sclerotic, where it is invested by the conjunctiva, as far as to the corneal margin, two vascular layers may be distinguished; a *deep episcleral or sub-conjunctival* layer, formed by the branches of the anterior ciliary vessels, and a superficial or *conjunctival vascular layer*, which only communicates with the former at the margin of the cornea.

The *anterior ciliary arteries*, after their emergence from the muscles, run very tortuously towards the margin of the cornea, near which they give off a number of fine episcleral branches, whilst their principal branches perforate the sclerotic. As a rule, two vessels proceed from each muscle, with the exception of the rectus externus, from which only one is given off. In many cases an artery to the temporal side proceeds from the palpebral vessels, and running in the connective tissue, perforates the sclerotic near the margin of the cornea.

The *anterior ciliary veins* are distinguished from the arteries by their smaller size (consequent on their much more insignificant perforating branches) and the straighter course of their coarser branches. Their episcleral branches, on the other hand, are larger than those of the arteries, as is usually the case where the two sets of vessels supply the same region. They communicate by a very rich plexus of fine veins with rather small polygonal meshes, which, on account of its position, has been named the *episcleral venous plexus*, and surrounds the cornea, forming a zone of about four millimeters in breadth.

The *episcleral branches of the arteries and veins* nearly correspond in their ramifications, the arteries being constantly finer, and running straighter than the veins in opposition to the relations of the trunks.

After giving off small *branches to the sclerotic*, they run with frequent subdivision and numerous arched communications

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in the second part of which (Max Schultze's *Archiv*, Band vi., pp. 261—362) the author maintains that the canal of Schlemm is a lymphatic cavity, and has no connection with the ciliary plexus, appeared after the above account was written. I must decidedly support my own view in opposition to that of M. Schwalbe.

to the margin of the cornea, and here give off fine branches at regular distances to the cornea, forming the

Anterior conjunctival arteries and veins. These pursue a recurrent course in the conjunctiva, supply the innermost zone of the conjunctiva, which has a breadth of from three to four millimeters, and anastomose with the peripheric or *posterior conjunctival vessels.* One or two veins constantly accompany each artery, in the latter case one being situated on either side of the artery.

The terminal branches of the episcleral vessels, frequently subdividing and anastomosing, run beyond and over the margin of the cornea, forming the *looped marginal plexus of the cornea,* which extends for a distance of one or at most two millimeters over the periphery of this membrane, and usually advance to a somewhat greater extent above and below than at the sides.

In the capillary loops we may discern a more slender ascending arterial limb, and a descending gradually widening venous limb.

In Man, after birth, no vessels penetrate into the substance of the cornea beyond this zone.

In the fœtus, J. Müller found vessels distributed over the whole anterior surface of the cornea. In many animals, as for example in the Sheep and Ox, vessels extend to a considerably greater distance over the surface of the cornea. In Oxen the superficial marginal loops, with flattened arches, can be very clearly distinguished from the vascular loops accompanying the nerves which penetrate much more deeply into the cornea. In the Sheep, Coccius saw these last extend as far as to the middle of the cornea. In Keratitis, newly formed vessels very frequently make their appearance, which may be situated in this membrane at all parts of its thickness.

3. Conjunctival Vascular System.

The larger peripheric portion of the scleral conjunctiva, the sulcus, and the tarsal portion, are supplied by the vessels of the lids, the arteriæ palpebrales medianæ et laterales, and the corresponding veins.

To the scleral conjunctiva pass numerous small arborescent branched vessels, arteriæ and venæ conjunctivæ posticæ (fig.

367, *d d'*). As is the case with the anterior conjunctival vessels, the arterial ramifications are here accompanied by one or two veins. They ultimately join the anterior conjunctival vessels. The meshes of the capillary plexus are tolerably wide, but become progressively finer towards the sinus palpebralis, and attain their highest development in the small papilliform elevations of the palpebral conjunctiva.

The posterior conjunctival vessels, and the veins in particular, are visible in the living eye of Man, forming small vessels capable of being moved with the conjunctiva, and distinguishable from the anterior ciliary arteries, not only by their course but by their brighter colour and their smaller callibre; the latter being of a more carmine tint, and not moveable with the conjunctiva. The difference in colour is due to the circumstance of the latter vessels being covered by the cloudy whitish conjunctiva. The anterior conjunctival vessels, like the anterior ciliary veins, are scarcely perceptible on account of their minute size, but come distinctly into view on irritation of the eye, when they undergo remarkable dilatation. The injection of the episcleral venous plexus produces a diffused bluish redness around the margin of the cornea, which in pathological states indicates a condition of irritation of the parts supplied by the ciliary vascular system; that is to say, of the uveal tract or of the cornea.

IV.

THE LYMPHATICS OF THE EYE.

By G. SCHWALBE.

THE lymph formed in the tissues of the eye is discharged from them in three directions. That portion which proceeds from the iris and ciliary processes collects in the anterior chamber of the eye, and finds its point of exit through the canal of Schlemm. With this system the canal of Petit is in direct communication; and these passages, together with the lymphatics of the conjunctiva and the canalicular plexus of the cornea, may be termed the anterior lymphatic system of the eye. All those parts of the globe that are situated behind the ciliary body discharge their lymph by two other tracts; the lymph proceeding from the choroid and sclerotic escaping at the points of emergence of the venæ vorticosa from the bulb, and that from the retina quite independently by a tract within the nervus opticus. The two last-named tracts may be collectively regarded as constituting the posterior lymphatic system of the globe; and with these we may include still another lymphatic space which exists between the two optic sheaths.

1. THE POSTERIOR LYMPHATIC SYSTEM OF THE EYE.

A. *The Canals for the discharge of the Lymph formed in the Choroid and Sclerotic.*

The lymphatics of the proper tissue of the sclerotic are developed to no greater an extent than are those of the vascular choroid. The lymph formed in these membranes passes into two large lacuniform spaces which are in direct communica-

tion with each other (fig. 369). One of these spaces (p) is situated between the sclerotic and cornea throughout the whole extent of these membranes, from the ciliary body to near the point of entrance of the optic nerve into the bulb. On account of its investing the choroid it has been termed the *perichoroidal space*. In Birds it forms a kind of lacuna, resembling the serous cavities in being bounded by two smooth walls. In Mammals the space is usually traversed by numerous trabeculæ,

Fig. 369.

Fig. 369. Diagrammatic representation of the posterior lymphatic tracts of the eye of the Pig, with the exception of the lymphatics of the retina. On the left the relation of the tendons inserted into the bulb, to the 'cavity of Tenon,' t, is exhibited; on the right, the latter is also shown near the insertion of the muscles. The lettering is for the most part referred to and explained in the text, but in addition a indicates a layer of fat between the retractor muscle and the supravaginal space; c, conjunctiva; $m\ r$, musculi recti; $m\ retr$, musculus retractor bulbi; v, external or fibrous sheaths of the optic nerve.

which in some instances, as in the eye of Man and of the Dog, may form quite a plexiform tissue, that has been named the *membrana suprachoroidea*. The portion of this tissue which remains attached to the sclerotic after detachment of the choroid has also been termed the lamina fusca. The peculiarity of structure of the plexiform tissue of the suprachoroidea is that it is

composed of numerous very flat lamellæ, the basis of which is formed of a rich plexus of elastic fibres. Closely connected with this plexiform tissue are numerous very flat and more or less branched pigment cells, which, when numerous, lie in close apposition, and resemble an epithelium. In many animals, as for example, in the Pig, in addition to these pigment cells, small flat colourless cells are constantly found to be present on both sides of the elastic lamella thus formed, or where this is firmly attached to the tissue of the sclerotic, on one side only, is a very thin glass-clear membrane, presenting at certain points ellipsoidal nuclei projecting beyond the general plane of the lamella. If these membranes are treated with solutions of nitrate of silver, containing from one-fourth to one per cent. of the salt, a beautiful plexus of dark silvered lines is brought into view, each mesh of which corresponds to one of the ellipsoidal nuclei. The elastic lamella of the supra-choroidea is then, it appears, covered by an endothelium, which differs but little from that of the lymphatic canals. Its presence may be demonstrated both on the outer surface of the choroid and upon the inner surface of the sclerotic, covering uniformly the whole perichoroidal system of cavities.

If injections be forced into the perichoroidal space, it will be found that the fluid passes into the second of the above-mentioned lacuniform lymphatic spaces at four points which lie close behind the points of emergence of the venæ vorticosæ. A careful examination of this region shows that the lymphatic vessel at first invests the vein as it passes obliquely through the sclerotic like a sheath (fig. 370), but shortly before reaching the external surface it separates from it, and lies on the inner and inferior side of the vessel. Its passage through the sclerotic is thus for the most part perivascular. Having reached the surface of the bulb, the injected fluid passes into a lymphatic cavity which exists between the sclerotic and the fascia of Tenon, and may be termed Tenon's space or cavity (fig. 369, *t*).

This is lined throughout by an endothelial layer of cells resembling that which lines the perichoroidal space. A network of dark silvered lines may easily be shown to exist on

the surface of the choroid with solutions of nitrate of silver. At those points where the ocular muscles are attached to the bulbus the continuity of the cavity of Tenon is interrupted; it is not, however, continued into the sheaths of the tendons, but is on that side completely closed. In Mammals, owing to the attachment of the musculus retractor bulbi (fig. 369, *m retr.*), it is divided into an anterior larger, and a posterior smaller cavity.

Fig. 370.

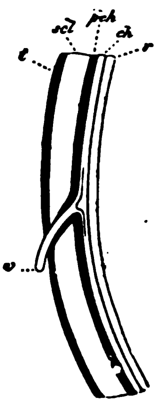

Fig. 370. Diagrammatic representation of the passage of a vena vorticosa, with its perivascular space, through the sclerotic, as seen in the Pig. *r*, Retina; *ch*, choroid; *pch*, perichoroidal space filled with injection; *scl*, sclerotica; *t*, Tenon's space; *v*, vena vorticosa.

At the posterior pole of the eye, and around the point of entrance of the optic nerve, the cavity of Tenon communicates with another lymphatic space which, like a sheath, invests the external fibrous sheath of the optic nerve, and on account of its position may be termed the *supravaginal space* (fig. 369, *spv*). This finally opens through the canalis opticus into the arachnoid space of the brain, which last, as is shown by injections beneath the dura mater, communicates directly with the lymphatics of the neck.

B. *The Lymphatics of the Retina.*

The lymphatics of the retina, as His (7, 8) discovered, form sheaths to the bloodvessels of this membrane. They are peri-

vascular canals of the same nature as those demonstrated by the same author in the brain and spinal cord. The veins and capillaries are completely invested by these lymphatic sheaths, whilst the arteries are probably only surrounded by them through a definite portion of their course. The injection of the retinal lymphatics may be accomplished by driving the fluid with considerable force into the bloodvessels. The latter give way at certain points, and the fluid then escapes through the rents into the perivascular canals. The discharge of the retinal lymph takes place in the optic nerve through the lamina cribrosa. According to His, the outer portion of the optic nerve contains a rich plexus of lymphatics, which, however, are here no longer perivascular.

A cavity which was described by Henle and Merkel (9), and which is situated between the membrana limitans interna and the optic-fibre layer of the retina, probably communicates with the perivascular canals of the retina. Lymph corpuscles are found in this position, but no injection of it has hitherto been successfully made.

The relation of the tissue of the vitreous to the lymphatic system is still unknown. Stilling (11) found that in the eye of the Pig a central vessel, perforating the vitreous from behind forwards, could easily be shown by dropping a solution of carmine upon the posterior surface of the latter, and this he regarded as a lymphatic canal. The perivascular canals of the hyaloïd of the Frog, described by v. Iwanoff (10), are the analogues of the perivascular canals of the retina of Mammals.

C. A lymphatic cavity which does not communicate with either of the two systems just described is found between the two optic sheaths throughout their whole extent from the bulb to the canalis opticus. On account of its position beneath the fibrous sheaths of the optic nerves, it may be termed the *subvaginal cavity* (fig. 369, *sbv*). It opens directly into the arachnoidal space. At the point of entrance of the optic nerve into the globe of the eye it extends to close beneath the choroid, though without entering into communication with the perichoroidal space. Its walls are lined by an endothelium, which is very easily separable in the form of small nucleated scales. The space is traversed by a rich plexus of delicate

connective-tissue trabeculæ, which are also enclosed by an endothelial sheath. Such sheaths may often be completely detached, and then appear as glass-clear membranes beset with elliptic nuclei.

2. The Anterior Lymphatic System of the Eye.

A. *The system of the anterior chamber of the Eye.*

The anterior chamber of the eye is a general receptacle for the lymph coming from the iris and ciliary processes, which flows into it at two points: from the canal of Petit through the capillary fissure between the pupillary border of the iris and the anterior surface of the lens; and from the ciliary body through the spaces between the trabeculæ of the ligamentum pectinatum.

The canal of Petit runs circularly round the margin of the lens, and extends laterally in the form of a narrow fissure, as far as to the ora serrata. Its lumen communicates by a series of fine fissures, which exist in the zonula ciliaris, close to the border of the lens, with the posterior, and through this with the anterior chamber of the eye. It may be easily injected from the anterior chamber, especially in the eye of the Pig. Under normal conditions, however, a current can only set in *from* the canal of Petit *towards* the anterior chamber of the eye, and not in the opposite direction, because in the latter case the iris forms a valve-like septum to the anterior chamber, which can only be overcome by such a change of form of the globe of the eye as results from increased intraocular pressure, which may be artificially produced by injections into the anterior chamber of the eye.

The principal channels discharging themselves into the anterior chamber of the eye open into this through the spaces between the trabeculæ of the ligamentum pectinatum, and conduct to it the lymph of a large portion of the ciliary body, and probably also of the iris. It is only in the eye of the Pig that a portion of this spongy region has been successfully injected with solution of Prussian blue thrown into the anterior chamber, and this has consisted of a fissure traversed by a plexus of connective tissue which extends circularly from

Fontana's canal, as far as to the posterior border of the ciliary body, and lies in this between the ciliary muscle and the pars ciliaris retinæ. In the eye of Man also fluids, when injected, penetrate at this point for some distance into the ciliary body. The trabeculæ of the canal of Fontana in Mammals, as well as the trabeculæ of the ligamentum pectinatum of Man corresponding to them, are everywhere invested by endothelial sheaths exactly resembling those which cover the trabeculæ of the subvaginal spaee.

The anterior chamber of the eye is lined throughout in front by the epithelium of the membrane of Descemet; behind, by the epithelium of the anterior surface of the iris, the two being continuous with each other in the angle of the chamber on the trabeculæ of the ligamentum pectinatum, yet so that fissures are here present, by means of which the plexiform system of Fontana's canal communicates with the anterior chamber of the eye. The latter discharges itself near the border of the membrane of Descemet, through the canal of Schlemm, into the venæ ciliares anticæ (15). This is shown by the fact that on injecting a solution of Prussian blue into the anterior chamber of the eye, these veins are always filled, but the lymphatics never. This repletion of the veins by injection occurs in the fresh eye of the Pig with a pressure not exceeding twenty millimeters of quicksilver, and demonstrates that the injection must reach the veins in well beaten paths, and that its entrance into the bloodvessels is not in any way rendered possible by rupture of the tissues. Nor can the intense blue injection of the veins be attributed to filtration, since the blue injection fluid never filtrates, as such, through vascular walls.

In order to ascertain the mode in which the communication of the anterior chamber of the eye in man with the veins is effected, it is necessary to examine meridianal sections of such eyes, made through the corpus ciliare, in which the veins have been filled by an injection driven into the anterior chamber. In such sections it may be observed that a short stria of the blue injection fluid extends from the anterior chamber of the eye just behind the margin of the membrane of Descemet, obliquely backwards and outwards to the canal of Schlemm.

The latter is also completely filled by the injection. In many preparations, injected vessels may also be observed in the sclerotic, which run from the canal of Schlemm, backwards and outwards through the fibrous membrane. Careful observation shows that these vessels are indubitably veins. Nevertheless, the canal of Schlemm must still be regarded as a lymph space, since the characters of its walls are essentially different from those of a vein. It communicates with the anterior chamber of the eye by means of a system of fine fissures. These fissures occur between the elastic circular fibres and fenestrated membranes, which extend from the margin of the membrane of Descemet, and form a modified prolongation of this membrane as far as to the posterior point of insertion of the ciliary muscle, and are continuous internally with the trabecular meshwork of the canal of Fontana. This peculiar tissue bridges over a groove situated on the inside of the anterior border of the sclerotic, where it joins the cornea, and converts this groove into a lacuniform circular canal, which is, in fact, the canal of Schlemm. The ciliary plexus of Leber is situated, as he himself states,* in the compact tissue of the sclerotic, just external to this groove.

In many cases, instead of *one* patent orifice, there are *two* or more, and thus a transition is effected to the eyes of Mammals, in which several small lumina are present at the same point, but which are always placed internally to the groove of the sclerotic.

The manner in which the canal of Schlemm is connected with the veins in its vicinity is still unknown. In all probability certain valvular arrangements exist, which prevent the passage of venous blood into the canal of Schlemm, under the normal conditions of pressure. If we consider what the consequences would be if the anterior chamber of the eye were to have in the lymphatics its proper discharge pipes, we shall readily understand the meaning of the above-described

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* *Anatomische Untersuchungen über die Blutgefässe des menschlichen Auges.* (Anatomical researches upon the bloodvessels of the eye of Man.) *Denkschriften der Kaiserlichen Akad. der Wissenschaften zu Wien. Math.-Naturwissensch. Classe*, Band xxiv., p. 316.

relations. Were the lymphatics the discharge pipes of the aqueous humour, it would be clearly impossible to preserve the relatively considerable pressure which exists in the anterior chamber of the eye, since with the low pressure of the fluids contained in the lymphatics a rapid discharge of the aqueous humour would occur, which could not be compensated for by the transudation of fresh fluid through the walls of the vessels, and the anterior chamber would collapse. This, however, is avoided by the opening of the lymphatics into the veins, through the intervention of the canal of Schlemm. Thus, owing to the circumstance that in the small veins the pressure is considerably higher than in the corresponding lymphatics, and further, owing to the resistance which the fluids have to overcome in their passage from the anterior chamber of the eye to the canal of Schlemm, in the narrow system of fissures, it becomes possible for the pressure in the anterior chamber of the eye to be preserved at its normal height, and for the entrance and discharge of fluid to be equalized.

B. The account of the cornea in this book may be referred to for a description of its canalicular system.

C. *The Lymphatics of the Conjunctiva.*

The lymphatics of the conjunctiva were discovered by F. Arnold (5), and were more exactly described by Teichmann (6). They arise at the margin of the cornea, where they form a delicate plexus of about one millimeter in breadth; more externally they are continuous with the wide-meshed lymphatic plexus of the sclerotic conjunctiva. The trunklets here soon become stronger, and usually run in a meridianal direction, anastomosing by means of numerous short, thin, transverse branches. According to Teichmann, a few branches proceed from the close plexus at the border of the cornea, in a meridianal direction towards its centre, forming a zone of about 0·1 of a millimeter wide. These perhaps correspond to the lymph-like structures described as lymphatic by Kölliker (3), His (1), and Sämisch (2).

According to Lightbody (4), the capillaries at the margin of the cornea are invested by lymphatic sheaths. I have not, however, been able in any case to satisfy myself of their presence.

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V.

THE VITREOUS HUMOUR.

By PROFESSOR A. IWANOFF.

The vitreous humour occupies the greater part of the cavity of the globe of the eye, and is surrounded posteriorly and laterally by the retina. The anterior surface is hollowed out into a slight fossa, in which lies the lens enclosed by its capsule. It presents a free surface from the margin of the lens to the apices of the ciliary processes, and this part looks towards the zonule of Zinn. The supposed interspace between this free part of the vitreous and the zonule of Zinn is termed the canal of Petit, which surrounds the whole free æquatorial border of the lens.

The dimensions and relations of this canal during life (canal godronné of Petit) have not been very accurately ascertained. Brücke describes the canal of much smaller size than is in accordance with the original description by Petit. Henke goes still further, and denies generally the presence of such an open space in the living eye. "It is not," he says,* "to be regarded as an open space, any more than the pleura, peritoneum, or articulations; but, like them, as a fissure between two free (serous) surfaces, moveable over one another, and without an intermediate space." Henle holds the same opinions; whilst Kölliker, on the other hand, believes that although the canal is certainly very narrow, it yet has a distinct lumen in the living eye, and contains a fluid.

My own researches support the view entertained by Henle, as in frozen eyes, at least, I was unable to discover any ice in the canal.

The vitreous is not, as has been hitherto generally admitted,

* Gräfe's *Archiv*, Band vi., Heft ii., p. 61.

surrounded by a special membrane, the so-called membrana hyaloidea. This membrane is in reality identical with the membrana limitans retinæ. It is a constituent of the retina, and is consequently applied immediately to the vitreous only so far as the retina extends, that is, to the ora serrata. From thence the membrana limitans is continuous with the pars ciliaris retinæ, but here meridianally running fibres lie between the vitreous and the limitans, which are known under the name of the zonula Zinnii, and these are intimately united both with the limitans and with the vitreous.

Near the ciliary processes the vitreous and the zonula separate from one another, so that the whole anterior surface of the vitreous which looks toward the canal of Petit and the lens is not covered by any special membrane, nor by a prolongation of the limitans, as Henle maintains, nor by a special membrana hyaloidea, as was formerly supposed.

Henle* has demonstrated the non-existence of the hyaloidea. In the meanwhile the name limitans hyaloidea is also not quite satisfactory in a strictly anatomical sense. That the limitans is an integral constituent of the retina is demonstrated in the clearest manner by pathological processes taking place in the vitreous: in consequence of which this last shrivels, and becomes detached from the retina.† In such cases the membrana limitans always remains *attached to the retina.*

In perfectly fresh specimens of the vitreous, and better still in those that have been hardened, the peripheric part exhibits distinct points of difference from the central. In the former a more or less obvious laminated structure is perceptible, whilst the latter appears to be homogeneous.

Stilling termed the central part the nucleus, and the peripheric the cortex. The homogeneous central portion, or nucleus, does not occupy the centre of the mass, so as to be uniformly invested by the concentric laminated cortex, but is pressed forwards towards the lens in such a way that the cortical substance becomes progressively thinner from behind forwards,

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* *Eingeweidelehre*, p. 661.

† A. Iwanoff, *Beiträge zur normal und pathologische Anatomie des Auges*, *Archiv für Ophthalmologie*, Band xv., Heft ii., p. 51.

and at the ora serrata the several concentric layers are so closely compressed together that the surface of the nucleus is here separated from the limitans only by a very thin but distinctly fibrous layer. The fibres of this layer run parallel to the surface of the vitreous, forming wavy fasciculi bearing some resemblance to the fibres of connective tissue. This entire layer thus modified ultimately curves inwards towards the optic axis, and covers the whole anterior surface of the vitreous.

Now, since we have here presented to us, not a single, but several compressed layers, though these are only loosely connected with each other, it is intelligible how easily we may come to the conclusion that there is a special membrane covering the vitreous and lying behind the lens, especially since the most superficial of these layers is perfectly smooth. The deeper-seated layers may sometimes in hardened eyes be separated from each other,—a circumstance that has led Hannover and Finkbeiner* to the conclusion that the hyaloid divides at the anterior surface of the vitreous into two laminæ in such a manner that behind the canal of Petit there is a second canal, the canal of Hannover.

In addition to the above-mentioned fibres resembling those of connective tissue that are met with in the anterior part of the vitreous, there are a considerable number of others like elastic fibres. They commence as early as at the æquator of the eye, in the form of extremely fine looped fibres, but are first seen in large numbers at the ora serrata; from this point, lying in close apposition to the limitans, they curve round into the pars ciliaris retinæ, and here form the commencement of the zonule of Zinn. A canal of about two millimeters in diameter runs forward through the vitreous from the papilla optica to the posterior surface of the capsule of the lens.

The difficulties that accompany the examination of the fresh vitreous induced all the earlier anatomists, who paid particular attention to this

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* *Vergleichende Untersuchungen der Stärke des Glaskörpers bei den Wirbelthieren*, (Comparative researches on the density of the vitreous humour in the Vertebrata,) *Zeitschrift für wissenschaft. Zoologie*, Band vi., p. 335.

subject, to adopt various methods of hardening. It was even believed that the diverse action of chemical reagents on the stroma and the mucous fluid occupying its meshes was capable of effecting their separation.

Pappenheim* was the first who adopted this plan. On hardening the vitreous in carbonate of potash, he found that the stroma of the organ consisted of laminæ running parallel to the surface, composed of very fine fibres and a homogeneous substance. Brücke† found that after the action of acetate of lead the vitreous appeared to be composed of a large number of very fine structureless membranes which were superimposed on one another like the layers of an onion, and ran parallel to the surface.

According to Hannover,‡ such a structure occurs only in Mammals. In Man the vitreous consists, according to him, of segments arranged radially around the optic axis, having some resemblance therefore to those of an orange. These appearances, however, are observed only in eyes that have been macerated for a long time in diluted chromic acid.

The observations of Hannover have been corroborated by Finkbeiner from the examination of hyaloids that had been treated with corrosive sublimate.

On the other hand, Bowman,§ Doncan, Virchow, Kölliker, and Henle obtained only negative results. Bowman and Doncan, in endeavouring to repeat and confirm or otherwise the observations of Hannover and Brücke, were unable to discover any membranes in the vitreous; in their opinion, as both state, the membranes and their arrangement are to be regarded as merely artificial products, resulting from the action of different reagents; Doncan entertained somewhat similar views to those held by Virchow and Kölliker, the former of whom considered the vitreous to be analogous to mucous tissue, and the latter to the connective tissues. At the same time he did not deny that this did not sufficiently explain either the existence of fluid and solid constituents in the vitreous or the entoptic phenomena. Henle also was unable to see any membranes, and simply describes the vitreous as a homogeneous substance of tenacious or cell-like nature.

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* *Spezielle Gewebelehre d. Auges*, p. 182. Breslau, 1842.

† Müller's *Archiv*, p. 345, 1843.

‡ Müller's *Archiv*, p. 467, 1845. *Das Auge, Beiträge zur Anatomie, Physiologie, und Pathologie dieses Organs*, p. 18. Leipzig, 1852.

§ Froriep's *Notizen*, No. 238, December, 1849, p. 274.

It is clear from this that the hyaloid membrane is nothing else than the limitans, which passes without interruption upon the pars ciliaris retinæ in front of the ora serrata, and Kölliker also holds this opinion. The limitans may be easily seen in meridianal sections through the pars ciliaris retinæ, supposing that the section runs exactly parallel to the course of the fibres of the zonula. In such preparations the limitans appears as a distinctly doubly contoured line, which divides by a very sharp line the pars ciliaris retinæ from the zonula.

In carefully made preparations the limitans may be detached for some distance as a fine membrane, both upon the zonula and on the pars ciliaris retinæ.

The views of Weber are quite peculiar, and unlike those of any other author. In his opinion the whole vitreous is composed of anastomosing cells forming a network, in the meshes of which a mucous fluid is contained.

Dr. Smith* has lately stated that the vitreous humour of Man, macerated for several days in water, and treated with carbolic acid, shows a concentrically laminated structure in its peripheric portions, whilst the central portion is radiated; the concentric laminæ, according to his account, are composed of coarse fibres, and the nucleus of stellate anastomosing cells. He observed also an open canal extending from the papilla optica to the posterior surface of the lens.

Bowman had already made similar statements in regard to the central portion. If the method adopted by Smith be pursued, it is difficult to determine what is and what is not to be regarded as an artificial product.

The great diversities of opinion on this subject held by different authors, as shown by this short historical account, are explicable on the one hand by the difficulties that present themselves in the examination of the fresh vitreous; and on the other by the differences that are presented by the various methods of artificially hardening it.

The membranes are the principal cause of discord, some maintaining that all the layers of the vitreous are separated from one another by membranes, whilst others, being unable to discover the membranes, deny in consequence the correctness of all the other observations. Now, although the membranes are really absent, this does not preclude the possibility of the existence of a laminated structure. Thin trans-

* D. Smith, Structure of the adult Human Vitreous Humour, *Lancet*, 19th Sept., Vol. ii., 1868, pp. 376—378.

verse sections of the vitreous of eyes hardened in Müller's fluid, split into layers which run parallel to the surface, and with the aid of high powers, after tinting with carmine, a finely granular mass makes its appearance in these layers, in the posterior part of this organ, together with a few scattered fine fibres. Anteriorly, towards the ora serrata the fibres become more abundant, and pursue a wavy course parallel to the surface. Even here, however, no traces of membranes are visible.

These statements respecting the structure of the vitreous have received fresh confirmation from the researches of Stilling,† which possess the advantage of having been exclusively made on the fresh vitreous, and are not therefore open to the objection that the conclusions arrived at are due to appearances artificially produced. According to Stilling, if sections be made through the fresh vitreous parallel to the optic axis, and a few drops of carmine be allowed to fall on the cut surface, a number of concentric furrows, varying from six to twelve, are formed in the periphery, whilst the centre, or nucleus, remains free from colour. The furrow forming the boundary between the cortex and the nucleus is, as a rule, the deepest, and is most quickly filled. Stilling does not give the relations of the cortex and nucleus quite correctly, since he was only able to apply his method to the determination of the coarser anatomy of the parts. He states that the cortex invests that part of the nucleus situated behind the ora serrata, so that the lens and zonula lie upon the latter alone. But, as we have seen above, the cortical portion, the several layers of which are closely compressed at the ora serrata, completely surrounds the nucleus, as is correctly shown in the illustrations of Hannover and Finkbeiner.

After Henle had demonstrated that no hyaloid membrane existed, he endeavoured to explain the existence of the membrane that, in his opinion, is found in the shallow groove covering the vitreous at this point, by assuming that the limitans, before it reaches the ora serrata, increases in thickness, and at the same time becomes altered in structure. He considered that it partially breaks up into fibres, which either pursue an irregularly tortuous course, like those of elastic tissue, or are parallel and wavy, like those of connective tissue ; in either case, however, being always remarkable for their extraordinary tenuity : and further, whilst the principal portion of these fibres or fasciculi of fibres

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* Stilling, *Eine Studie über den Bau des Glaskörpers, Archiv für Anatomie,* Band xv., Heft iv.

extend over the surface of the vitreous, a few penetrate into its interior, where they are soon lost.

According to the same author, the superficial fibrous tissue of the limitans hyaloidea divides at the point where the orbicularis ciliaris begins to enlarge into the corpus ciliare, into two laminæ, of which one passes inwards to form the hyaloidea of the shallow groove, whilst the other passes outwards to the pars ciliaris retinæ, in order to form the zonula.

The researches above given show, in opposition to those of Henle, that all those changes to which the limitans is subjected, take place in the peripheric layers of the vitreous, whilst the limitans itself remains unaltered, and becoming progressively thinner, passes simply from the ora serrata to the pars ciliaris retinæ. It thus not only takes no part in the formation of the urceolate groove of the hyaloidea, which, as has been above shown, does not exist, but the part it takes in the formation of the zonula is more than doubtful. I at least have never been able to discover this relation, whilst the origin of the zonula from the vitreous may be very easily observed.

It only remains therefore to determine whether the limitans is actually continuous with the pars ciliaris retinæ. Henle himself admits that if we consider the fibrous layer of the zonula as the anterior lamina of the limitans, the latter again splits into two layers at the apices of the ciliary processes, and that in some cases he has even seen the hyaloid membrane extend beyond the origin of the fibres of the zonula on the orbiculus ciliaris.

As regards the development of the zonula, we now know that it does not exist in the embryo, so long as the vessels investing the capsule are present, although at this period the limitans is already completely developed. The zonula first appears at the time when the capsular vessels atrophy, and as their atrophy proceeds becomes progressively more and more distinct.

But if the limitans passes unaltered from the ora serrata over the pars ciliaris retinæ, it is self-evident that it cannot possibly form a quantity of fibres of the zonula, and beyond this, by further division, the membrane of the quoit-like groove.

All this confusion originates in the fact being overlooked, that the superficial layers of the vitreous become already altered in their structure in front of the ora serrata, and are intimately fused with the limitans and the retina. At the same time the coalesced parts are not altogether inseparable since, in some pathological cases, and even in healthy eyes, treatment with alkalies will very often effect

the detachment of the vitreous with the zonula from the membrana limitans.

In the year 1814, Martegiani described a funnel-shaped depression in the vitreous at the point of entrance of the optic nerve, which he named the "area."

This "area Martegiani" is really the commencement of the canal which has been incorrectly designated the canalis hyaloideus Cloqueti. Cloquet never saw and never depicted the canal in adults; he only describes the course of the capsular artery in the fœtal vitreous.

Hannover describes the canal better, but states expressly that he has never found it open, and thus really knew nothing of the existence of a proper canal.

The account given by Finkbeiner * is not clear; of the existence of an open canal in any fully developed eye of Mammal or Man he really says nothing. He describes at length only the eye of the Ox, in which two elongated areæ unite to form a solid cord traversing the vitreous.

The presence of this canal as a patent tube existing throughout life in the eye all Mammals and of Man, and gradually increasing to the period of complete development of the whole eye, was first demonstrated by Stilling, who described the method by means of which it can be demonstrated in the fresh eye.

The cells of the vitreous are situated only in its external superficial layers; in the deeper layers we meet only with derivatives from them, that is to say, with nuclei and shrivelled vesicles. Though their form is very various, they can all be classed under three principal groups.

1. Round cells with large nuclei, the latter surrounded by coarsely granular protoplasm. These occur chiefly in the anterior portions of the vitreous, especially in children, in whom they often contain several nuclei.

2. Fusiform and stellate cells. These are met with throughout the peripherical portions of the vitreous. The stellate cells usually possess long, fine, ramified processes, which are beset with varicose dilatations.

3. A very characteristic form of round cells, which contain in their interior a large, round, and perfectly transparent

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* *Loc. cit.*, p. 332.

vesicle. In fully developed cells of this kind a single vesicle only exists, which completely fills the entire cavity, and only leaves a little space at the periphery for a nucleus surrounded by a small quantity of protoplasm. Sometimes two vesicles occur, separated from each other by a straight line. In other cases there are several vesicles which appear to be surrounded by a common sheath, the contour of which is perfectly spherical.

The vesicles just described are not only found in the round cells, but are seated also on the processes of the stellate cells; where they sometimes attain a colossal size, exceeding that of the cells themselves. We meet with these at all periods of life, though chiefly in old people, and in the posterior portions of the vitreous.

All these cells possess the property of contractility. They change their form and perhaps also their place. The contractility of the round cells containing vesicles is less in proportion to the size of the vesicles, and the more consequently the protoplasm has diminished.

The views in respect to the existence and the nature of the cells are as various as those on the structure of the stroma.

We are indebted to Virchow for the first special investigations that were made upon the cells. In the embryo of a Pig four inches in length he found, distributed at tolerably regular distances through the homogeneous intercellular substance, round, nucleated, sometimes multinucleated and coarsely granular cells.

According to Kölliker, the cells occur especially in young persons; he saw them indeed in some adults, but scattered and indistinct, and chiefly near the lens and hyaloid membrane. Weber, on the other hand, found stellate anastomosing cells throughout the whole vitreous. Hannover and Finkbeiner describe an epithelium covering the hyaloid membrane, and this, according to the last-named author, invests also the several septa in its interior. The same view is also entertained by Coccius. Ritter observed an epithelium with ramified cells only on the internal surface of the hyaloid, but no cells, on the other hand, within the vitreous.

The fibres of the zonula, as has been already stated, spring from the vitreous, and from that part of it which has not yet reached the ora serrata retinæ. The zonula-fibres arise near

this latter, and, lying at first beneath the surface of the vitreous, ascend towards the ora serrata, and become applied in the form of extremely fine fibrils to the membrana limitans retinæ, with which they are in close contact; in this way the vitreous and limitans are so intimately connected at the ora serrata that it is impossible to separate the retina from the vitreous, portions of the vitreous remaining constantly adherent at the ora. But just as on the one hand it may be clearly demonstrated that the zonula-fibres arise from the substance of the vitreous behind the ora serrata, so, on the other hand, it may be shown that the territory of origin of the zonula does not terminate at this line. The origin of the zonula-fibres from the corpus vitreum may also be shown to take place for some distance *in front* of the ora, and consequently towards the ciliary processes, so that here also the zonula and the vitreous do not form isolated structures.

The zonula Zinnii first appears to be completely differentiated from the vitreous at a distance of from four to five millimeters from the ora. As it passes towards the lens it is separated from the pigment layers of the smooth portion of the corpus ciliare, as well as from that of the processus ciliaris, by the pars ciliaris retinæ and by the everywhere demonstrable membrana limitans. Nevertheless, the zonula is not prolonged to the apices of those ciliary processes that project furthest forwards, but speedily separates itself from them in order to pass to the æquator of the lens. Having arrived at this point, the fibres of the zonula break up in the form of a brush, and by means of these brush-like processes the zonula becomes attached to the anterior and posterior capsule of the lens.

The first appearance of the fibres of the zonula in the vitreous is in the form of wavy fasciculi of extremely fine fibrils. At the surface of the vitreous the several fibrils composing each fasciculus coalesce to form a single fibre; and the fibres thus composed are the finest of those forming the zonula proper. At their point of emergence from the vitreous, the fibrils (which have not yet coalesced) are intimately connected with the limitans. Thus it happens that if an attempt be made to strip off the zonula in a backward direction from the corpus ciliare, it tears through at this point of the limitans. This is

the foundation of the incorrect statement that the fibres of the zonula are the direct prolongation of the limitans. If, however, the vitreous with the zonula and lens be macerated for several weeks in a ten per cent. solution of common salt, the connection between the zonula fibres and the limitans is loosened, and the isolation of the two structures is rendered easier.

The fibres of the zonula, as they extend forward towards the ciliary processes, coalesce in part to form fibres which progressively increase in thickness, so that the free portion of the suspensory ligament of the lens (which aids in forming the posterior wall of the posterior chamber of the eye) contains the thickest fibres; in great part, however, they also run nearly unchanged in diameter from the ora serrata to the æquator lentis. It has already been stated that at this latter point they again break up into extremely fine fasciculi.

In a meridianal section of the eye the zonula presents the appearance of resting with a triangular base upon the æquator lentis. This triangular area is completely occupied by the terminal fibrils of the zonula fibres, but at the same time contains no cavities, and has not been mistaken by any one except Merkel for the canal of Petit.

The fibres of the zonula are neither connective-tissue nor elastic fibres. Their relations, both chemical (as with acids and alkalies) and physical, show that they are different from either. It would be rash, however, as has recently been done, to regard them as being muscular. Comparative anatomical and embryological researches, which can alone be appealed to in order to settle the real nature of these fibres, are at present wanting.

The zonule of Zinn forms the anterior wall of the canal of Petit. The posterior wall is formed by the smooth surface of the vitreous. The tissue of the vitreous is condensed at this part, just as the membrane of Bowman is a condensation of the tissue of the substantia propria of the cornea. There is here no independent membrane or hyaloidea. The canal of Petit commences at a distance of from four to five millimeters from the ora serrata, and reaches not only to the æquator of the lens, but for two millimeters on the posterior capsule of the lens towards the posterior pole of that body.

It is difficult to determine whether there is really a space

filled with fluid and corresponding to the canal of Petit; in other words, whether this canal possesses a lumen in the living eye. We may rather admit, with Henke and Henle, that the anterior and posterior walls of the canal of Petit in the living eye, without being fused together, are in contact, or only separated by an extremely thin layer of fluid. Even, however, if the canal of Petit, as such, does not exist, the disposition of parts above described will enable the physiological rôle subserving accommodation ascribed to it to be fulfilled.

VI.

THE LENS.

By PROFESSOR BABUCHIN.

The lens, an organ which in form and in transparency closely resembles an ordinary glass bi-convex lens, but which varies in shape in different animals, is one of the most important constituents of the dioptric apparatus of the eye. In Man its antero-posterior axis is one-third less than the transverse diameter, whilst in many animals the lens is almost spherical. To whatever extent the form and dimensions of the lens may vary, its elementary structure and plan are alike in all Vertebrata. It is everywhere composed of two constituents, the cellular elements, which form the body of the lens (parenchyma lentis, proper substance of the lens), and the investing membrane, which, exhibiting no further differentiation of structure, completely invests it, and is termed the capsule of the lens.

The substance of the lens may be regarded as composed of two layers. One of them, the anterior, is very thin, and begins to increase in thickness near the æquator, either very gradually, as in Man or Mammals, or rather rapidly, as in Birds and the scaly Amphibia. The posterior layer, on the other hand, is very thick, and becomes gradually thinner from the axis of the lens, where it is thickest, towards the æquator. Near the æquator the two layers coalesce, a little more forward in some animals, in others a little further backwards, or, to describe it more accurately, they are continuous with one another by a rounded border. Except at this border, the two above-described layers may be everywhere easily separated from one another,

though there is no measurable intervening space between them (fig. 371).*

Fig. 371.

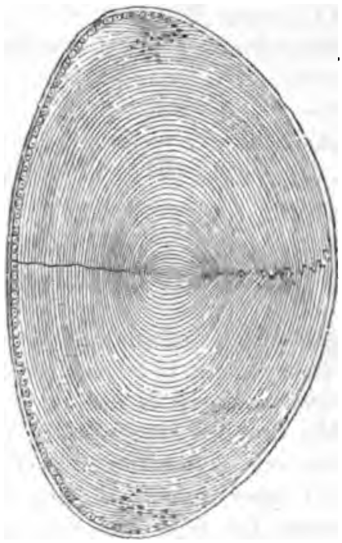

Fig. 371. Meridianal section through the axis of the lens in Man.

The anterior layer is composed of flattened polygonal cells, which are as transparent as glass, and when fresh, as in animals that have just been killed, are perfectly structureless. After the lapse of some time, or after treatment with various reagents, these cells become cloudy, and it then becomes possible to distinguish clearly their contour and their central round or oval nucleus. The cells vary in size in different animals; in Man they measure about 0·032 of a millimeter (Becker). Near the border of the lens they are columnar or almost cylindrical in form, and are arranged perpendicularly to the surface of the lens; farther on they are still taller, and assume a more oblique position, inclining with their inner ends towards the anterior surface of the lens; they at the same time become more conical, their broad basis being turned towards

* All the illustrations accompanying this essay have been drawn by Sernoff, from his own preparations.

the surface of the lens. Still farther backwards the cells become yet longer, and their direction still more oblique, and their anterior extremities curve to meet the ends of the adjoining above-described cells. All these relations may be much better understood from the adjoining fig. 371, and still better from fig. 372 B, which shows the parts just described under a high power. Thus originates the junction of the anterior thin layer of the body of the lens with the thicker posterior layer. The transition of the epithelial cells of the anterior layer into the fibres of which the posterior is composed, results therefore simply from the elongation of the cells of the former.

In successful preparations the epithelial cells of the anterior layer preserve at all points, whatever changes they may undergo in form, the characters of true cells; that is to say, they always possess a well-marked nucleus surrounded by proto-

Fig. 372 A.

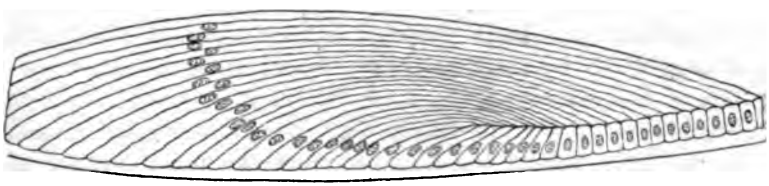

Fig. 372 A. Meridianal section through the margin of the lens of the Rabbit, showing the transition of the epithelium into the fibres of the lens.

plasm. Neither I nor Dr. Sernoff,* who by his investigations under my inspection has materially assisted in explaining the true structural relations of the lens, were ever able to discover at any part of the lens, in place of true cells with well-marked protoplasm and nucleus, "the sharply defined irregular nuclei of various sizes," the so-called formative cells of Becker,† which, according to his description, lie in close apposition at the point of attachment of the zonula, have but little surrounding protoplasm, and often exhibit distinct indications of fission.

* *Ueber den Mikroskopischen Bau der Linse bei Menschen und Wirbelthieren* (On the microscopic structure of the lens in Man and other Vertebrata), *Dissert. inaugural.*, 1867.

† Becker, *Archiv für Ophthalmologie*, 1863.

The transition of the epithelial cells into the fibres of the lens does not occur in this way in all animals. A modification which Heinrich Müller found to occur in Birds and in the Chamælon, and which I and Sernoff observed in many scaly Reptiles, is that, in opposition to what takes place in other animals, the flat epithelial cells become higher, and not far distant from the anterior pole assume the characters of columnar cells, then gradually elongate as far as to the plane of the æquator, and from thence onwards shorten, though they never again present the character of flat epithelial cells. These constitute the vertically placed radial fibres of the lens, which had previously been noticed by Treviranus and Brücke in the lens of the Bird. All these fibres, or, more correctly speaking, all these elongated cells, appear more or less regularly hexagonal on section; their peripheric extremity is broader than their central, and is not hexagonal, but rounded on section. At this end there is usually a single round or oval sharply defined nucleus. In the anterior half of the lens these cells adhere firmly by their anterior extremities to the inner surface of the capsule of the lens; but in the posterior half, as Sernoff has shown in Birds, they become separated almost immediately behind the æquator from the inner surface of the capsule, so that around the whole lens a flat circular canal is formed, which is filled with a structureless mass. Sernoff and I have met with an exactly similar canal to this of Birds in the embryoes of many Mammals and of Man, situated behind the point of transition of the anterior epithelium into the fibres of the lens. In Man it exists even for some time after birth, and in Birds it is persistent throughout life.

Whilst, as already stated, the radial cells become shorter at the posterior part of the lens, they change their direction, and from being radially arranged become obliquely placed, and thus are gradually converted into meridianally placed lenticular fibres, just as in Mammals.

We shall now proceed to consider in what mode the fibres of the lens participate in the formation of the posterior thick layers of the nucleus, and consequently of the most important part of the whole structure. The process is essentially the same in all Vertebrata. Flat fibres unite to form curved

lamellæ, which, covering one another concentrically like the coats of an onion, augment in size from the point of transition of the epithelial cells into fibres towards the pole, then diminish in the direction towards the nucleus of the lens, until they finally attain their smallest dimensions at the centre of the lens or a little posterior to it. It is here necessary to remark that the fibres of the first more superficially situated layers, which form

Fig. 372 B.

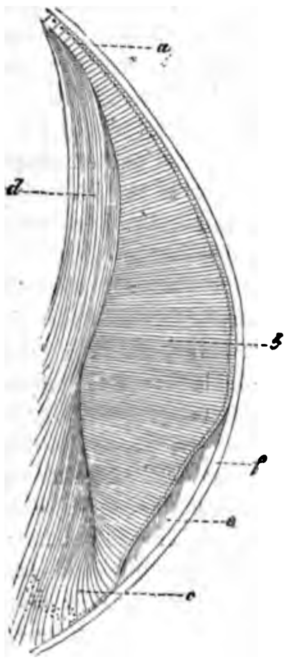

Fig. 372 B. A meridianal section through the border of the lens of the Fowl. *a*, Epithelial cells ; *b*, vertical or radial fibres ; *c*, their transition into the meridianal ; *d*, meridianal fibres ; *e*, structureless mass ; *f*, capsule.

the equatorial portion of the lens, and are consequently situated close to the point where the fibres pass into epithelial cells, are curved inwards; that is to say, their convexity is turned towards the axis of the lens, whilst their anterior extremities are in contact with the epithelial layer, and their posterior extremities touch the capsule. The fibres of these layers are

flatter and more slender at their centre than at their extremities (fig. 372 A). Their curvature alters as they approximate the axis. The outer ones are straight, whilst those situated more internally become more and more S-shaped, till they are ultimately so much arched that both their anterior and posterior extremities bend inwards towards the pole. In proportion as the fibres approximate the axis they very gradually become longer, in consequence of which the fibres of each successive more deeply situated layer projects somewhat beyond the superjacent ones, so that the ends of these last, still adhering to the anterior and posterior walls of the capsule, cover one another like the tiles of a roof.

But these characters refer only to the fibres of the several peripheric layers of the lens. The extremities of the remaining fibres, which belong rather to the inner layers of the lens, pass to the poles and axis, and meet here with the extremities of those fibres which come from the opposite parts of the lens.

This junction varies in different animals. It is most simple in some Fishes and Amphibia, as in the Cod (Brewster), Triton (Harting), Salamander (Harley), Frog (Becker), and in Birds, where the fibres of the lens belonging to one and the same layer begin from the æquator, gradually become more slender and, like the intervening spaces of the meridians of the earth, meet one another with pointed extremities at one point of the axis of the lens. In some Fishes, as for example in the Torpedo, the posterior extremities of the fibres also join or meet in the axis, whilst the anterior ones of each layer form a raphé by their apposition, which with low powers appears as a straight line on the anterior surface of the lens, at right angles to the axis, from which the fibres run in a radiating manner towards the æquator. And inasmuch as the raphé of the successive internal layers likewise forms straight lines with gradual shortening towards the centre of the lens, it may be said that in these cases the anterior extremities of the fibres of the lens of all the layers meet in one (otherwise very irregular) plane which perhaps has the form of a triangle, the slightly arched base of which is turned towards the anterior surface of the lens, whilst its vertex is lost in the nucleus of the lens.

In the greater number of Fishes and Amphibia, and in some Mammals, as in the Rabbit, Hare, and Dolphin, both the anterior and the posterior extremities of the fibres of the lens terminate in the manner jüst described, so that the posterior and anterior raphés have the appearance of straight lines. These, however, do not run in the same direction, but cut one another at right angles. In these cases the fibres do not embrace the entire half, but only a portion of the lens, in the following manner. If, for the sake of example, the anterior extremity of a fibre commences at the end of the anterior raphé, it terminates, after passing backwards in the direction of a meridian, at the middle of the opposite raphé, and consequently in the axis of the lens. If a fibre commences at the centre of the anterior raphé, it passes to the extremity of the posterior one. In the human fœtus and in the newly born of many, perhaps the greater number of animals, the junction of the fibres both on the anterior and posterior surface of the lens presents the following complicated relations. The raphés form a kind of star, composed essentially of three rays, the point of junction of which corresponds to the axis of the lens. The angle comprised between any two of the rays is 120°. The rays of the anterior and of the posterior stella are not placed in the same plane, but so that each anterior ray is intermediate to two rays of the posterior star; in other words, there is an angle of 60° between the several rays of the anterior and posterior stars. Lastly, there are animals in which, as in the adult Man, the stella is composed of a larger number of rays. Thus, for example, in the anterior stella of Man as many as nine rays may be counted, and a still greater number in the posterior (fig. 373 A and B). Not unfrequently the rays divide at their extremities; but even with this complication those of the anterior and posterior stella do not lie in the same planes. This complication affects only the superficial layers of the lens; in the deeper layers these complicated stellæ, as is well known to occur in the adult Man, become converted into the three-rayed stella.

All the earlier inquirers (Werneck, Hannover, Kölliker, Henle, Leydig, Becker, and others) believed that the ends of the fibres did not come into immediate contact with the rays of the star, but that there was an intervening space, which was

filled by a structureless or granular mass that was considered to be a constant constituent of the lens. Now as the stella passes through all the layers, fissures should in that case exist corresponding to the number of the rays of this star, and should penetrate, both upon the anterior and the posterior surfaces of the lens, vertically inwards to the nucleus. Becker* attributed peculiar importance, in regard to the physiological functions of the lens, to these fissures, which he considered to be filled during the life of the animal by a semi-fluid

Fig. 373 A.

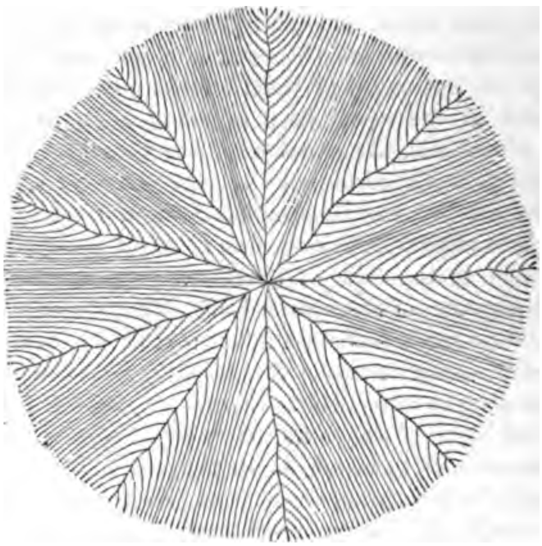

Fig. 373 A. Anterior stella of the lens.

homogeneous transparent substance. He believed that these fissures communicated, by means of minute openings found in their walls, with special canals which expanded between the fibres of the crystalline lens (interfibrillar passages), so that the contents of the stellate fissures could discharge themselves into the canals, or *vice versâ*, during the changes which the lens underwent in the act of accommodation for varying distances. Kölliker however stated, in his *Mikro-*

* *Archiv für Ophthalmologie*, 1863.

skopische Anatomie, p. 711, that he had been able to find but few traces of any such substance in lenses in which the fibres were well preserved. Hensen regarded the interfibrillar passages of Becker as artificial products; and Sernoff has lately demonstrated that neither the stellate fissures, with the substance supposed to be contained in them, nor the interfibrillar passages, have any existence. This last-named observer has shown also that in quite fresh and also in carefully hardened specimens the fibres of the lens directly abut against

Fig. 373 B.

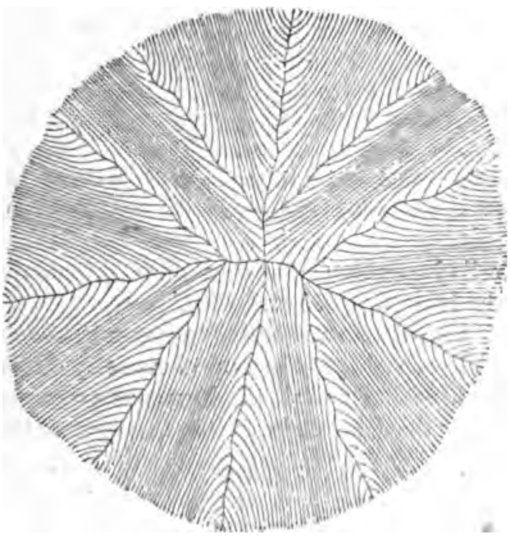

Fig. 373 B. Posterior stella of the lens.

one another in the stellæ, the radii of the star when examined with high powers appearing in the form of sinuous lines (fig. 374). Carefully made sections of the lens in various directions show also clearly that no kind of intervening space exists between the fibres. It thus appears that both Becker's structureless stellate substance and his intercellular passages are simply artificial products, the former probably depending on a splitting of the ends of the lens fibres, and the latter on a dislocation of the fibres consequent on the sections having been roughly and carelessly made.

As regards the fibres of the lens, we know that although their length, thickness, etc., differs in the different layers, they have always the character of flattened bands, which appear on section as more or less slender and elongated hexagons. Hence, when the section is carried through several fibres in their natural position, we obtain a honeycomb-like appearance, the

Fig. 374.

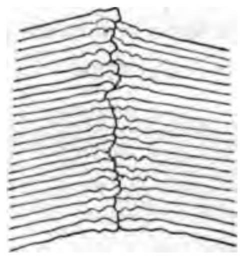

Fig. 374. Horizontal section through a raphé in the eye of the Ox, to show how at this point the fibres of the lens abut against each other.

individual cells being elongated in a direction parallel to the surface of the lens (figs. 375 and 376).

From such transverse sections it is apparent how the margin of one fibre is received into the angle formed by the borders of the adjoining fibres. In Birds the hexagons are very long and narrow, proving that the fibres of the lens are in them much

Fig. 375.

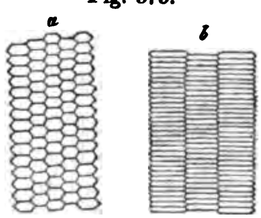

Fig. 375. Vertical sections through the fibres of the lens in their natural position; *a*, from the Calf; *b*, from the Fowl.

more flattened than in Mammals. I consider the so-called radiating fibres in Birds to belong to the epithelial layer of the lens. In Fishes the fibres are so flat that it is difficult to determine with accuracy what form they present on transverse section.

As a general rule, the superficial fibres of the lens are broader and thicker than those more deeply placed. Moreover the area of the transverse section of the fibres is not the same throughout their whole length. In Man the fibres which are situated at the border of the lens, and, as above mentioned, are curved outwards, are thicker at their extremities than at their centre. Those fibres, on the other hand, which lie nearer to the nucleus, and whose ends are curved towards the axis of the lens, become gradually more and more attenuated from their centre or æquatorial portion towards the two extremities, though they slightly expand again at their apices. The greater number of the fibres of the lens in Mammals terminate at some point of the surface with thickened or expanded extremities. If the fibres of the lens reach to the axis (as from what has been stated above is seen to occur in some Fishes, Amphibia, and Birds), or if they meet in one line only (as in the Rabbit, Hare, etc.), it is self-evident that they cannot expand, but must gradually become narrower from the æquatorial region, to terminate either, as in the former cases, in a very pointed extremity, or, as in the latter, by a more or less blunt point.

The contour line of the fibres also varies. In all animals the superficial ones have always smooth, the deeper, on the other hand, uneven or dentated edges. This is the case in Man, especially at the extremity of the fibres. The dentation is more marked in Mammals, and still more in Amphibia and Birds. In the greater number of Fishes, as Brewster long ago pointed out, the fibres are beset with long and regularly disposed dentations (fig. 376).

However long the teeth may be, they diminish regularly in size towards the extremities of the fibres, and ultimately form mere wavy elevations. The teeth of one fibre are directed towards those of another, with which they probably interlock. In Mammals and Birds, however, this certainly does not occur.

Those fibres which are more or less deeply situated near the border of the lens, all possess a single sharply defined oval nucleus, in the centre of which is a round nucleolus. The position of the nucleus varies in different fibres. In closely

adjoining fibres, however, they are not very remote from each other; so that in meridianal sections of the lens they form a more or less broad zone of varying curvation—the so-called Meyer's zone, which constitutes an immediate prolongation of a regularly arranged series of epithelial nuclei (fig. 372 A and B.

Ritter* discovered short nucleated fibres, or rather cells, in the centre of the lens in the Frog, which he believes represent the formative elements of the fibres of the lens. Sernoff found similar cells, but in the Frog alone. If we take into consideration that these cells are very resistant, that their surface is in

Fig. 376.

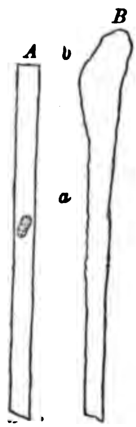

Fig. 376. Isolated fibres of the lens; *A*, from Man; *B*, from the Fish; *a*, central part; *b*, extremities.

general very rough, that nuclei are not found in their interior, or if present are irregularly dentated, it will appear much more probable that they are the remains of old embryo cells, which have only attained a certain grade of development, than that they are young formative cells, the formative material for the fibres of the lens.

The consistence of the fibres of the lens varies in accordance with the layer in which they are found. The superficial fibres are usually very soft and delicate, and easily break up in

* *Archiv für Ophthalmologie*, Band xii., Abtheil. i., p. 17.

macerating fluids into detached drops of various sizes (hyaline drops), but partly also into a finely granular or structureless mass. This breaking-up occurs also spontaneously after death, and inasmuch as it chiefly affects in the first instance the extremities of the fibres, it is intelligible that the products of the breaking up must principally accumulate in the stellæ of the lens. Hence these products were formerly held to be normal constituents of the lens. Moreover, under certain circumstances, vacuolæ form in the fibres, and their borders then appear just as though they had been eroded. The deeper the fibres lie, that is, the nearer the centre, the more resistant do they become, and the less are they acted on by reagents.

Authors usually admit the existence of a sheath to the fibres of the lens, and call them by another name, to wit, lens tubules. But it is a matter of great difficulty to demonstrate the presènce of this sheath, especially in the extremely thin dentated fibres of Fishes, and the grounds on which authors found their statements are still more untenable than those which are advanced to prove the presence of a membrane in the blood corpuscles. The presence of longitudinal and transverse striæ in the fibres of the lens has also been maintained; but this striation is so rarely visible, and presents so many irregularities, and so much variability in its arrangement, that no conclusions can be drawn from it in regard to the minute structure of the fibres, and they should rather be looked upon as accidental wrinklings and irregularities.

Mineral acids, alcohol, and the act of boiling cause the fibres of the lens to become hazy, whilst their contours are rendered more distinct. This depends on the circumstance that their principal chemical constituents are of an albuminous nature; consisting, in fact, chiefly of globulin, with a certain quantity of albuminate of potash, and ordinary ser-albumen. Other materials that have been ascertained to enter into the composition of the lens fibres are a little fat, with traces of cholesterine, about one half per cent. of ashes, and sixty per cent. of water. The qualitative characters, no doubt, vary with the layer from which the fibres are taken; for, apart from the fact that the central fibres are more resistant, the nucleus of the lens becomes much harder than the superficial layers under the

same reagents; so that in Fishes, for example, the nucleus remains transparent, hard, and difficult to cut. The cloudiness of the fibres of the lens, and the formation of vacuolæ in their interior, are occasioned by the action of reagents which withdraw water from them.

As regards the origin of the lens, and the mode of development of its fibres, it is obvious from the above-described direct transition of the anterior epithelial layer of the lens into the posterior fibrous layer, that each fibre of the lens is simply a colossal and greatly elongated epithelial cell, and the history of development shows further that the persistent portions of the body of the lens arise from the epidermoid external layer of the embryo.

The body of the lens, as has been already stated, is entirely surrounded by a structureless, smooth, and transparent membrane. It is only in those cases where the membrane is very thick that in transverse sections of hardened specimens a longitudinal striation can be recognized, favouring the idea of its being laminated. It is not everywhere of equal thickness. In all animals the anterior half, and indeed that portion which is bounded by the line of attachment of the zonule of Zinn, is also thicker than the posterior; in Man it is about twice as thick. It is thinnest at the posterior pole. The substance of the capsule is tolerably resistant and very elastic; on section it rapidly rolls up backwards. Several authors have found epithelial cells upon the posterior surface of the capsule of the lens, which probably resulted from the circumstance that the inner surface of the anterior capsule has been described as covered with epithelial cells. It would nevertheless be more natural, from the developmental history of the lens, to reverse the matter,—to say, namely, that the epithelium which forms the anterior layer and the direct continuation of the posterior, as well as this last itself, is covered by the capsule. It would appear that either the impressions of those posterior extremities of the fibres of the lens which directly abut against the capsule, or the spherical bodies which arise from the breaking-up of these ends, have been taken for epithelial cells. It is extremely difficult to give an account of the development of the capsule. It has been maintained that it is the product of the excretion

of the epithelial cells, as well as of the fibres of the lens, but no satisfactory evidence of this has been given. I have very frequently seen that the first rudiment of the capsule, which is uncommonly delicate, is folded and remote from the surface of the lens, which is very difficult to connect with the idea of its origin by excretion. In preparations made by Sernoff, who has long been occupied with this question, I have had the opportunity of seeing (in the embryoes of Fowls) that tho capsule of the lens contains nuclei, and it would perhaps be more correct to classify it with the metamorphosed connective-tissue formations. The question is obviously not yet settled.

VII.

THE CORNEA.

By ALEXANDER ROLLETT.

THE cornea of the eye of vertebrate animals is composed of several layers of tissue, presenting different characters. The anterior and posterior surfaces of the layers run nearly parallel to the surface of the cornea, as far as to the margin of the cornea (*limbus corneæ*), where they are bounded by the conjunctiva, the sclerotic, and the ligamentum pectinatum iridis.

LAYERS OF THE CORNEA. (Fig. 377.)

The layers of the cornea, enumerated from without inwards, are as follows:—

1. The external epithelium of the cornea (fig. 377, *a*—*b*). This is a laminated pavement epithelium.

2. The proper tissue of the cornea (substantia propria, seu fibrosa corneæ, lamellated or fibrous tissue of the cornea, fig. 377, *b*—*c*). The connective tissues of the cornea are included in this layer.

3. The membrane of Descemet (membrane of Demours, membrana humoris aquei, vitreous lamella of the cornea, lamina elastica posterior of Bowman, internal basement membrane of Henle, fig. 377, *c*—*d*). This is a sharply defined lamella, usually of homogeneous aspect.

4. The endothelium of the membrane of Descemet (internal epithelium of the cornea, epithelium of the membrane of Descemet, epithelium humoris aquei, fig. 377, *d*—*e*). This is a simple layer of flattened cells.

The succession of layers just described as existing in the cornea may be easily followed in vertical sections of specimens

that have been dried or hardened in chromic acid, Müller's fluid, or alcohol, or which have been frozen. The layers vary in thickness, the thickest layer being formed by the cornea proper, which, in Man, is about one millimeter in thickness at the outer border, whilst it is somewhat thinner at the centre.* The external epithelium stands next to this in thickness, being in Man 0·03 of a millimeter thick.† After this comes the membrane of Descemet, with a thickness at its centre, in adults,

Fig. 377.

Fig. 377. Meridianal section through the cornea of an adult Man; the eye having been hardened in Müller's fluid. The section was stained with carmine, and rendered transparent with oil of cloves.

of 0·006—0·008, and at its periphery of 0·01—0·012,‡ and lastly, the endothelium of the membrane of Descemet. The appearances presented in such sections by the external epithelium, the membrane of Descemet, and the endothelium, require

* Brücke, *Anatomische Beschreibung des menschlichen Augapfels*, p. 9. Berlin, 1847.

† Henle, *Handbuch der Eingeweidelehre*, p. 605. Braunschweig, 1866.

‡ H. Müller, *Archiv für Ophthalmologie*, Band ii., Abtheil. i., p. 48.

no further elucidation (fig 377). It is less easy to indicate the nature of those presented by the proper tissue of the cornea.

If we regard its features as they appear in a section made from an eye hardened in Müller's fluid, and stained with carmine (fig. 377, *b*—*c*), it may be said to possess a fasciculated or banded structure. The substance forming the matrix appears to be divided, though very irregularly, into striæ (lamellæ, Bowman's lamellæ, secondary lamellæ of Henle),* which run longitudinally in the direction of the lines of section of the surfaces of the cornea, the division being occasioned by elongated interspersed bodies or corpuscles running in the same direction as the striæ, which are sometimes broad, and are sometimes so attenuated as to appear like simple lines. As the broader parts become narrower, they are continuous with the striæ, or are gradually lost in the matrix. The dilatations are either completely occupied by elongated bodies (corneal corpuscles of Toynbee and Virchow), which are darker than the matrix, and more strongly tinted than it, or these corpuscles are separated on one or both sides from the matrix, and are smaller than the cavity in which they are enclosed. Near the outer surface (fig. 377), but at a certain distance from the superficial epithelium, these fusiform markings succeed each other more quickly than in other parts of the section, and between this richly corpusculated layer and the epithelium is a band of the matrix which is broader than any of the rest (lamina elastica anterior of Bowman, anterior basement membrane of Henle),† (fig. 377, b—b^1). In its broad, uniform aspect it resembles the membrane of Descemet, but is always thicker than this, and never so sharply defined. Its contour line is also never so sharply defined towards the external, as the membrane of Descemet is towards the internal epithelium. The internal contour line of this layer is also less sharply defined when it is continuous with the matrix in the bridges formed by the matrix between the above-mentioned closely compressed corpuscles. This feature is very well marked in sections carried through the centre of the human cornea. A

* *Loc. cit.*, p. 592.
† *Loc. cit.*, p. 605.

somewhat different appearance is presented at the periphery, in consequence of the projection of sinuous fibres of what appears to be the matrix proceeding from the deeper layers towards the epithelium, from whence they again return (fibræ arcuatæ; supporting fibres; Stutzfasern of Henle).* In the corneæ of certain animals, as, for example, of the Ox, this arrangement is constant in all parts of the cornea.

In the thin cornea of small animals, as in that of the Frog, the same sequence of layers may also be observed, if the cornea be removed by cutting round its margin with a sharp pair of

Fig. 378.

Fig. 378. Layers of the cornea of the Frog, as seen in a fold of the tissue lying in aqueous humour. *a b*, External epithelium; *b c*, tissue of the cornea proper; *d*, membrane of Descemet; *e*, endothelium of the latter.

scissors, and its folds are then examined under the microscope in aqueous humour. The appearances presented are seen in fig. 378.

The minute anatomy of the several layers of the cornea just alluded to must now be described in detail.

The Tissue of the Cornea proper.

The proper tissue of the cornea belongs to the group of connective tissues, cells, and fasciculi of fibrils; the latter, traversing the cornea in various directions, constitute its microscopic elements, together with peculiarly formed cavities in which

* *Loc. cit.*, p. 604.

the cells of the cornea are contained. Forms also occur in the corneal tissue similar to those which may be demonstrated in fibrillar connective tissue, to which the proper tissue of the cornea has the greatest resemblance. The developmental history of the two tissues have also many features in common.*

THE CELLS OF THE CORNEA.—Two kinds of cells have been distinguished in the cornea.

A description of one of the forms of cells, to which little attention has been paid, was originally given by Toynbee ;† but Virchow,‡ in his investigations first brought them so prominently into notice, that since that date they have formed a rich field of research and discussion amongst histologists, under the name of corneal corpuscles or Toynbee-Virchow's corneal corpuscles. v. Recklinghausen§ first called attention to the presence of a second form of cell in the tissue of the cornea. These will receive consideration hereafter.

ON MIGRATING OR VAGRANT CELLS, AND ON THE INFILTRATION OF THE CORNEA WITH SUCH CELLS.—The migrating cells (moving corpuscles of the cornea)|| may be recognized by their active amœboid movements.¶

They may readily be found in the cornea of the Frog, when this has been recently removed from the animal as a whole, and placed under the microscope with the membrane of Descemet looking upwards in the aqueous humour, in a moist chamber.** Their number varies in different corneæ. They become more sharply defined, and are seen more distinctly,

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* See this Manual, Vol. i., pp. 47, *et seq.*, and 70.

† *Philosophical Transactions*, Part ii., p. 179, 1841.

‡ *Würzburger Verhandlungen*, Band ii., pp. 154 and 314. *Cellular Pathologie.* Strube, *Der normale Bau der Hornhaut und der pathologischen Abweichungen in demselben,* (The normal structure of the cornea and its pathological changes,) *Dissert. inaug.* Würzburg, 1851.

§ *Ueber Eiter und Bindegewebskorperchen*, (On pus and connective-tissue corpuscles,) Virchow's *Archiv*, Band xxviii., p. 157.

|| v. Recklinghausen, *loc. cit.*, p. 168, *et seq.*

¶ See this Manual, p. 54, *et seq.*

** v. Recklinghausen and Engelmann, *Ueber die Hornhaut des Auges*, (On the cornea of the eye,) p. 3, *et seq.* Leipzig, 1867.

owing to their increased lustre, after being macerated in the fluid for a few minutes.

Their rapid alterations of form are exactly similar to those of the amœboid cells of the blood of the Frog, or the free pus corpuscles found in the aqueous humour of that animal. They are of a remarkably elongated and attenuated shape in the tissue of the cornea. They move from place to place; a phenomenon that is only intelligible when, in addition to the mobility of the cells, the permeability of the medium (the corneal tissue) in which they are observed, is clearly recognized. Referring the latter for subsequent consideration, we shall here accept the permeability of the tissue as a fact, and follow the cells alone.

Migrating cells are found at all depths of the corneal tissue. The course they pursue varies, and is usually very devious,* though sometimes rectilinear. In the latter case the passage of a cell across the field of a Kellner's microscope occupies from half an hour to a whole hour (v. Recklinghausen).

Migrating cells may be seen in the fresh cornea of other animals besides the Frog. Amongst Mammals, observations have been made in respect to them by v. Recklinghausen on the Rat, Rabbit, Dog, Ram, Ox, and Pig; but it is requisite in the case of the thicker corneæ to make sections parallel to the surface with a sharp knife. The movements of locomotion are not in all cases, but sometimes just as evident as in the Frog.

The migrating cells of the cornea of the Frog change into highly refracting roundish bodies provided with only short processes or projections, when placed in a moderately strong solution of sugar (v. Recklinghausen, Engelmann). The number of migrating cells undergoes considerable increase, if inflammation be produced in the cornea by producing an ulcer with nitrate of silver (purulent infiltration). The same occurs also if inflammation be excited by any other cause (traumatic keratitis.)

As soon as the amœboid characters of the pus corpuscles found in the aqueous humour after ulceration of the cornea had been observed, proving the accuracy of the view previously maintained by Virchow, that pus corpuscles are identical with white blood corpuscles, it was also observed that the pus corpuscles found in parts of the cornea infiltrated

* v. Recklinghausen, *loc. cit.*, pp. 157—171.

with pus possess the same mobility, and that similar but sparingly distributed amœboid cells occur also as migrating cells even in the healthy cornea.*

We must not omit, in an account of the cornea, to enter into special details in regard to the mode of origin of the amœboid cells met with in purulent infiltration of the cornea, since, as we shall hereafter see, the researches on this subject play an important part in the controversies on the peculiarities and the significance of that form of cell in the cornea which was formerly characterized as corneal corpuscles or as Toynbee-Virchow corneal corpuscles.

I desire in the first place to call attention to the appearances which may have been considered to show that the haziness of the cornea in traumatic inflammation is due to a proliferation of the cells (nuclei) contained in the cornea.†

When the examination of the corpuscles of the cornea began to be more carefully considered, attempts were made to ascertain the nature of the changes occurring in it in inflammation; ‡ and through such examinations continued by His, § Weber, || Rindfleisch, ¶ Langhans,** it was endeavoured to give a more detailed expression of the view of the origin of the pus corpuscles from the corpuscles of the cornea. Lastly, after the amœboid character of migrating cells had been established, it was pointed out how those of the cornea, either directly or owing to the division of the cells, could undergo conversion into such migrating cells.††

It was shown at the same time that the corneæ of various animals exstirpated whilst still living, or just after death, and which had been

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* v. Recklinghausen, *loc. cit.*, pp. 157—171.

† Bowman, Lectures on the parts concerned in the operations on the Eye and on the structure of the Retina, p. 29, fig. 5. London, 1849.

‡ Virchow, *Ueber parenchymatöse Entzündung*, (On parenchymatous inflammation,) Virchow's *Archiv*, Band iv., p. 259. Strube, *loc. cit.*

§ *Beiträge zur normalen und pathologischen Histologie der Hornhaut*, (Essays on the normal and pathological histology of the cornea,) p. 45. Basel, 1856.

|| *Zur Entwickelungsgeschichte des Eiters*, (On the mode of development of pus,) Virchow's *Archiv*, Band xv., p. 475.

¶ *Untersuchungen über die Entstehung des Eiters*, (Researches on the origin of Pus,) Virchow's *Archiv*, Band xvii., p. 239.

** *Das Gewebe der Hornhaut in normalen und pathologischen Zustände*, (The normal and pathological conditions of the cornea,) *Zeitschrift für rationelle Medicin*, 3 Reihe, Band xii., p. 22.

†† v. Recklinghausen, *loc. cit.*, p. 181.

preserved in the lymph sacs of living Frogs, absorbed by their edges into their substance, from the fluid surrounding them, numerous amœboid cells as immigrants.*

A few years subsequently it was stated that the pus corpuscles found in keratitis in the living animal, like those met with in the inflammation of other organs, were to be regarded as chiefly composed of immigrant white blood corpuscles which had wandered into the corneal tissue.†

It soon appeared that direct observations of a similar nature had been made long before by Waller,‡ though they had been forgotten. These observations referred essentially to the permeability of the vascular walls for blood corpuscles,—a process that has been demonstrated by direct observation of the passage of red§ and white blood corpuscles|| through the vascular walls.

It thus appeared that the origin of the numerous pus corpuscles met with in the cornea in purulent infiltration was to be sought in the blood, and not in the corpuscles of the cornea, since the latter in the infiltrated parts of the cornea are still present in a wholly unaltered condition (Cohnheim). The purulent infiltration, it was concluded, must always begin at the border of the cornea—at that part, namely, to which, as we shall hereafter see, vessels are distributed, and where granular pigments, as anilin blue and cinnabar introduced into other vascular regions, reappear in the pus corpuscles of the cornea.¶

At the same time, in opposition to all this, it has been shown that in the excised and ulcerated corneæ of Mammals and Frogs preserved in one of v. Recklinghausen's propagating cells, an accumulation of actively moving cells occurs around the irritated spot. Here we are compelled to regard the cells as the descendants of the corneal corpuscles that have disappeared.** As regards the cloudiness that proceeds from the border of a cornea made to undergo ulceration in the living animal (His, Cohnheim), the mobile cells must indeed be

* v. Recklinghausen, *loc. cit.*, p. 183.

† Cohnheim, *Ueber Entzündung und Eiterung*, (On inflammation and suffocation,) Virchow's *Archiv*, Band xl., p. 1.

‡ *Philosophical Magazine*, Vol. xxix., pp. 271 and 398, 1846.

§ Stricker, *Sitzungsberichte der Wiener Akademie*, Band lii., p. 379.

|| Cohnheim, *loc. cit.*, p. 38, *et seq.*

¶ Cohnheim, *loc. cit.*

** F. A. Hoffmann, *Ueber Eiterbildung in der Cornea*, (On the formation of pus in the cornea,) Virchow's *Archiv*, Band xlii., p. 204.

considered to be derived from the blood, but the cloudiness around the point of irritation must be set down to the proliferation of the corneal corpuscles.*

On the other hand it was maintained, as showing the non-participation of the corneal corpuscles in the formation of pus, that no cloudiness appears in the cornea of the Frog, after the application of a caustic, if the blood of the animals had previously been completely displaced (as Cohnheim believed) by a 0·75 per cent. solution of common salt injected in the course of one or two hours. This is quite in favour of the non-participation of the corneal corpuscles in the formation of pus.†

Soon, however, the results of new investigations were published, which had been undertaken by Norris and Stricker,‡ in which the proliferation of the corneal corpuscles in inflammation, and their transition into migrating cells, were maintained in the most decisive manner, and illustrated by several drawings.

Thus two different origins are attributed by different authors to the migrating cells of the cornea; from the blood alone; from the corneal corpuscles alone, or from both coincidently.

We shall recur to this subject after we have described the peculiarities and origin of the second form of cell found in the cornea.

THE CELL-PLEXUS OF THE CORNEA—CORNEAL CORPUSCLES—CORNEAL CORPUSCLES OF TOYNBEE AND VIRCHOW—STELLATE (RADIATED MULTIPOLAR) CORNEAL CORPUSCLES—MOTIONLESS CORNEAL CORPUSCLES (v. Recklinghausen)—FIXED CORPUSCLES OF THE CORNEA (Cohnheim).§ These structures are cells destitute of a membrane or cell-wall, but provided with nuclei. Each cell has a flattened body and a similarly shaped nucleus. The short diameter of the flattened cell is perpendicular to the surface of the cornea, or deviates but little from this direction. The surfaces of the little plates

* F. A. Hoffmann, *loc. cit.*, pp. 209—217.

† Cohnheim, *Ueber das Verhalten der fixen Bindegewebs-Körperchen bei der Entzündung*, (On the behaviour of the fixed connective-tissue corpuscles in inflammation,) Virchow's *Archiv*, Band xlv., p. 333.

‡ *Studien aus dem Institut für experimentelle Pathologie in Wien. Herausgegeben von Stricker*, pp. 1, 18, and 31, 1870.

§ *Loc. cit.*, p. 180.

are thus presented if we look vertically from the surface through the cornea, or examine under the microscope sections made parallel to the surface. The borders of the flattened cells then appear irregular in consequence of a variable number of processes being given off from them in different directions.

These processes branch, and at the same time become more and more delicate; they are not all in the same plane with the flattened body of the cell, but pass both upwards and downwards. The processes given off from adjoining cells intercommunicate, forming a cell-plexus that traverses the cornea. The meshes of this plexus vary in form, but the trellis-work formed by the processes is often very regularly rectangular.

The substance of the cells, and that of their processes, presents either a smooth and homogeneous or a finely granular aspect.

The foregoing general description of the cell-plexus formed by the corneal corpuscles in the tissue of the cornea corresponds to a definite condition of the cells, and recurs in precisely the same form in the corneæ of Man and of the most diverse animals, as in the Frog, Newt, Dog, Cat, Ox, Rabbit, Guinea-pig, Pig, Sheep, Hedgehog, Bat, Rat, Mouse, and Fox.

As regards the form and arrangement of the cells and their processes, this account of the corneal corpuscles agrees with that generally adopted since His * described the beautifully marked forms obtained from specimens prepared with wood spirit.

In regard to the cells and processes formed and disposed as has been described above, we have given in sufficient detail the views suggested by the new cell doctrines. Whilst immediately after the publication of His's well-known work, the cell-plexus was regarded by many histologists, as by His himself, as a hollow plasmatic plexus, the cells and their processes being provided with membranes like those ascribed by Virchow to the plexuses of the connective substance; we, on the other hand, see in it a protoplasmatic plexus (Kühne) which extends throughout the entire substance of the cornea.

This statement is not, however, entirely unopposed. The

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* *Würzburg. Verhandlungen*, Band iv., p. 90, *et seq.*

cell-plexus of the stellate corneal corpuscles may also be regarded as an artificial product. In fact, the cells of the cornea may be glass-clear laminæ of an elastic nature, with oval elongated or irregularly excavated borders, and a simple or rarely double nucleus. These cell laminæ may resemble endothelial cells; and as the presence of flat nucleated cells has been demonstrated (by Ranvier)* in the tendons, it may be urged that an arrangement of flat cells, disposed side by side, plays a more or less exclusive (?) rôle in the structure and functions of connective tissue.†

Our own researches into the nature of the corneal corpuscles have led us to the conclusion that they cannot be regarded as constituting such elastic laminæ, in opposition to the older view representing them as forming a plexus of radiating and intercommunicating corpuscles. We shall now proceed to place before the reader the results of the investigation of these cells in the living tissue.‡

If a living cornea with a small margin of sclerotic be rapidly excised, and examined under the microscope in aqueous humour, it appears as perfectly homogeneous as the transparent, glass-clear, fresh cornea; § the figures represented in fig. 379 only appearing where there are depressions or folds (Engelmann).

After a short time the migrating cells come into view, and then the corneal corpuscles, which appear in the first instance as dull stars‖ or as spindle-shaped bodies,¶ in which neither granules nor nuclei can be discerned.

Sooner or later, however, small granules and nuclei, which are for the most part elongated, become visible, and render the

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* *Archives de Physiologie normale et pathologique.*

† Schweigger-Seidel, *Ueber die Grundsubstanz und die Zellen der Hornhaut des Auges*, (On the matrix and cells of the cornea,) *Sitzungsberichte der K. Sächsischen Gesellschaft der Wissenschaften. Math. phys. Classe*, pp. 320, 323, and 328, 1869.

‡ v. Recklinghausen, *loc. cit.*, p. 171, Taf. ii., fig. 2. Kühne, *Untersuchungen über das Protoplasma und die Contractilität*, pp. 123—131. Leipzig, 1864. Engelmann, *loc. cit.*, pp. 3, 4, *et seq.*

§ Engelmann, *loc. cit.*, p. 4. Stricker, *loc. cit.*, p. 1.

‖ v. Recklinghausen, *loc. cit.*, p. 171. Engelmann, *loc. cit.*, p. 5.

¶ Kühne, *loc. cit.*, pp. 124 and 125.

corneal corpuscles still more distinct. The close agreement in the co-efficients of refraction of all the elements of the fresh cornea is thus gradually lost after excision. At first the corpuscles can be only discovered with difficulty and in parts, but subsequently they become much more distinct. The cornea of the Frog, taken from eyes that have been preserved for a considerable period in a moist chamber, are especially well adapted for the demonstration of the corneal corpuscles.*

Fig. 379.

Fig. 379. Corpuscles of the cornea, from the recently excised cornea of the Frog, preserved for twenty-four hours in the fold of the membrana nictitans. The corpuscles and processes represented all lie on the same plane.

When the excised cornea of the Frog has been preserved for twenty-four hours in the fold of the membrana nictitans,† the corpuscles appear as they are represented in fig. 379.

In such specimens, by different focussing, the whole plexus formed by the corpuscles traversing the cornea may be readily followed.

An excellent method of exhibiting the cell-plexus in the cornea consists in the application of chloride of gold.‡ A

* Kühne, *loc. cit.*, pp. 130 and 131.

† Stricker, *loc. cit.*, p. 36.

‡ Cohnheim, Virchow's *Archiv*, Band xxxviii., pp. 346—349.

fresh cornea from the Frog should be macerated in a solution containing 0·5 per cent., until it is thoroughly stained of a yellow colour; it is then to be exposed to the light

Fig. 380.

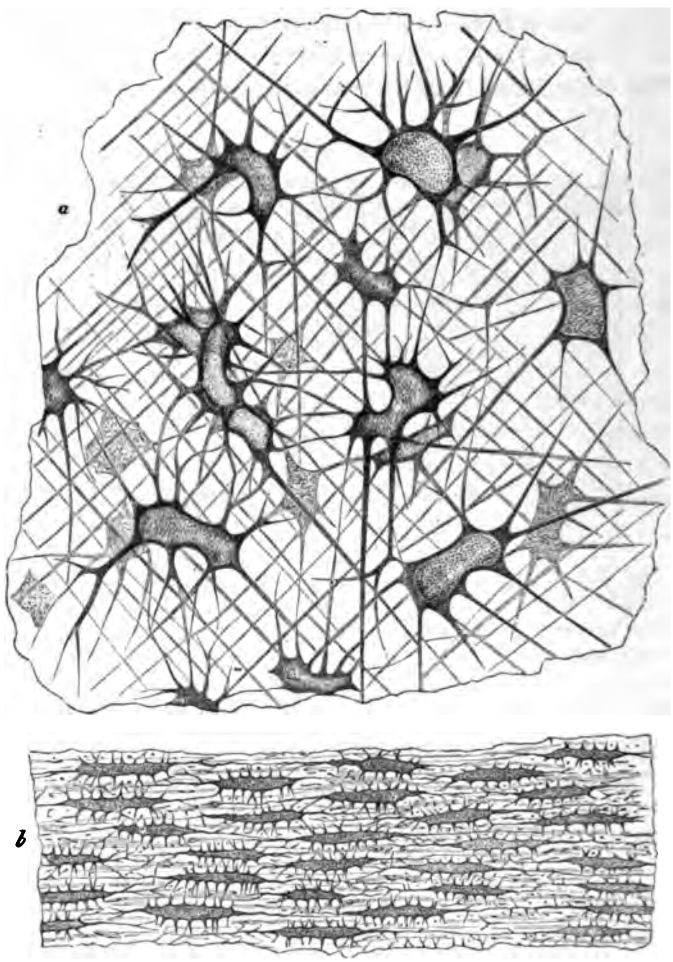

Fig. 380. *a*, Corpuscles of the cornea of a Frog, treated with chloride of gold, and seen from the surface; *b*, corpuscles of the cornea of a Frog, treated with chloride of gold, as seen in a vertical section.

in water acidulated with a little acetic acid, when it rapidly assumes a reddish or bluish colour. If now, in the course of a few days, and with the addition of a little glycerine, the specimen be examined under the microscope, after the anterior epithelium has been brushed off, the most beautiful results in regard to sharpness of outline and minute detail are obtained, the cell-plexus appearing tinted of a red or blue colour by the reduced gold (fig. 380, *a*).

Thin vertical sections of such corneæ may be made with great success, showing the course of the processes of the corpuscles. These may be observed traversing the cornea in all directions. When seen lengthwise, they appear still in connection with the nucleated central mass, or we may meet with longitudinally, obliquely, or transversely divided fragments (fig. 380, *b*).

It is also very instructive to tease out both surface and vertical sections of corneæ stained with chloride of gold, and to examine the behaviour of the cells and their processes, and this is particularly requisite in regard to the mutual relations of the cells and matrix which will be presently discussed.

Gold preparations of the cornea of the most diverse animals give, when successful, images that essentially correspond to the cell-plexus of the cornea of the Frog, which is so far important, as we have the best opportunity in the cornea of this last-named animal of satisfying ourselves that the corpuscles make their appearance in precisely the same manner, except that they are coloured, as when other methods of preparation are employed. And just as in the corpuscles of the earlier mentioned preparations, so also in those of the gold preparations, a thorough and complete similarity is discernible between the cell-substance collected around the nucleus and the substance of the processes.

There are yet other methods of impregnating the cornea with metallic salts, as by treatment with nitrate of silver (Coccius,* His,† v. Recklinghausen),‡ and also by impregnation with iron,

* M. C. A. Flinzer, *De Argenti nitrici usu et effectu, etc.* Lipsiæ, 1844. *Dissert. inauguralis.*

† *Loc. cit.*, p. 67; Virchow's *Archiv*, Band xx., p. 207; *Schweizerische Zeitschrift für Heilkunde*, Band ii., No. 1.

‡ Virchow's *Archiv*, Band xix., p. 451; *Die Lymphgefässe und ihre*

lead, and the salts of copper, and subsequent treatment with sulphuretted hydrogen, sulphide of ammonium, cyanide of potassium, and the like.* These methods likewise all tend to prove the existence of the above-described protoplasmatic plexus; the nature of the action, however, in each case is only capable of being understood when we consider at the same time the material or matrix in which the cells occur, a subject upon which we shall have occasion to enter into more detail hereafter.

From the foregoing observations it will be seen that the chloride of gold deserves the highest praise as a means of bringing the corneal corpuscles into view; nevertheless there is still another method I would recommend, which consists in immersing the cornea in aqueous humour, and placing it in a cell,† where it can absorb the vapour of iodine.

The cornea assumes a brown tint in the iodine cell, and the epithelium can then be easily brushed away. On removing it, but replacing it if requisite in the cell, the cell-plexus of the cornea appears with a distinctness that is little if at all inferior to the gold preparations. The migrating cells are also brought very clearly into view, in consequence of their becoming stained of a beautiful brown colour. The absorption of the iodine vapour takes place with great rapidity, and its operation can be followed with the microscope. The method is absolutely certain for the fixation of transitory conditions of the cornea, and cannot therefore be sufficiently commended. Every one who is accustomed to work with chloride of gold knows that, however excellent the results when the preparation is a successful one, something is defective in the method, since it not unfrequently occurs that even when the greatest care has been taken partial or complete failure happens, and that for certain investigations this constitutes a very great disadvantage to it. Not only is the simple representation of the cell-

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Beziehung zum Bindegewebe, (The lymphatics and their relations to connective tissue,) p. 4, *et seq.* Berlin, 1862.

* Leber, *Zur Kenntniss der Imprägnationsmethoden der Hornhaut und ähnlichen Gewebe*, *Archiv für Ophthalmologie*, Band xiv., pp. 300—316.

† Described by me in the *Untersuchungen aus dem Institute für Physiologie und Histologie in Graz.*, pp. 15 and 18. Leipzig, 1870.

plexus excellently attained with iodine vapour, and not only are we able by means of control-researches with perfectly fresh masses of protoplasma elsewhere obtained (mature and embryonal connective tissue), which may be examined whilst still living, to give an explanation of the successive effects of iodine in bringing the cell into view; but we shall hereafter be able to refer to this method for the decision of other moot points in regard to the cornea.

Let us now turn back to consider in greater detail, and whilst quite fresh, the cells composing the cell-plexus of the cornea. It has already been mentioned that when perfectly recent, they are throughout so completely identical in their refractile power on light with the matrix of the cornea, that it is impossible to discover them under these circumstances. It is important to know, however, that if the cornea has once commenced to lose its perfect transparency, which gradually takes place when it is kept under observation in a moist chamber, and immersed in aqueous humour, the corneal corpuscles do not immediately lose their vital properties.

In point of fact, it is at this time that their contractility is to be witnessed. The spontaneous changes of form under the conditions in which they were seen by Kühne,* and which, according to his statements, are so deliberate that they can only be demonstrated by a camera lucida, I have not been able to observe.

I must, however, substantiate the statement that induction shocks of electricity are capable of producing contraction of the corneal corpuscles. I must consequently take the part of Kühne, in opposition to Engelmann and others; my description of the phenomena differing from his to a much less extent than theirs.

Experiments made elsewhere† induced me to try the effects of applying a few powerful opening-induction shocks as a stimulus. This was accomplished by the aid of a Rühmkorff's coil (with a primary coil of 160 turns, iron core, and a secondary

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* *Loc. cit.*, p. 125.

† Golobew, *Archiv für Mikroskopische Anatomie*, Band v., pp. 55 and 56; and this Manual, pp. 41, 72, and 73.

coil of 6,245 turns) rendered active by two large chromic-acid and carbon elements, the poles coupled in one and the same direction. The primary coil was entirely covered by the secondary.

A series of shocks thus applied, caused the corpuscles to diminish in size when seen from the surface; partial retraction and attenuation of the cell processes were also observed. The most remarkable result of the electrical excitation is not however presented by these phenomena in the protoplasm of the cells, but rather by the sudden appearance in the cornea of the contours of v. Recklinghausen's serous canal system (lacunæ of the cornea), so that I must regard the electrical excitation of the cornea as a veritable *experimentum crucis*, proving the existence of these much-disputed structures.

The visibility of the serous canals depends on the above-mentioned contraction of the protoplasm of the cells of the cornea.

We shall describe with greater minuteness the consequences of electrical excitation hereafter, when speaking of the serous canals.

The lively movements however may here be mentioned, which are observable in the corneal corpuscles of inflamed corneæ, when the fresh membrane is exposed to a constant current of blood serum,* as well as the retraction of the processes of the corneal corpuscles after the application of a four per cent. solution of phosphate of soda,† a phenomenon which cannot be regarded as a mere shrinking, because the radiated form is preserved with stronger solutions.

In the foregoing remarks, sufficiently definite statements may be found in respect to the corneal corpuscles to demonstrate that the views entertained by Schweigger-Seidel respecting them cannot be regarded as correct.

We shall hereafter recur to two experiments of Schweigger-Seidel, which lead to the isolation of its laminæ; namely, the injection of the cornea by simple puncture with iodine serum, syrup, or diluted alcohol, and the boiling of the cornea in

* Stricker and Norris, *loc. cit.*, p. 4.
† v. Recklinghausen, Virchow's *Archiv*, Band xxviii., p. 179.

alcohol acidulated with hydrochloric acid. The lines of Hoyer in serous canals, on which Schweigger-Seidel supports his statements, will also be subsequently described.

Considering the various means that we possess to bring the protoplasmatic plexus of the cornea into view, and further, in consideration of the typical manner in which this plexus makes its appearance in all the corneæ that have been examined, it will appear extremely rash to every one who applies analogical conclusions as aids to thought, where this is really permissible, that Schweigger-Seidel, in opposition to every analogy, endeavours to explain the radiated corneal corpuscles as illusory cells caused by the excretion of a peculiarly distributed interfibrillar cementing substance.

THE BEHAVIOUR OF THE CORNEAL CORPUSCLES IN INFLAMMATION OF THE CORNEA, AND THE ORIGIN OF THE MIGRATING CELLS.—To decide the just-mentioned controversy it is of fundamental importance to determine the behaviour of the corneal corpuscles in inflammation. Before we quitted the subject of the migrating cells we alluded to the various views which have lately been advanced upon their origin. We were led finally to the essay of Stricker and Norris.*

The latter have demonstrated that ulcerated corneæ, treated at various periods after the application of the caustic with chloride of gold, which colours the migrating cells as beautifully as the corneal corpuscles, give images which show a considerable proliferation of nuclei in the corneal corpuscles. These corneal corpuscles become converted into clusters of nuclei; and the examination of other specimens makes it extremely probable, from the relative proportion borne by the corneal corpuscles to the migrating cells at the same spot, that the latter develop from the former through the intermediation of these multi-nucleated masses.

Ulcerated corneæ examined in the iodine cell give the most beautiful examples of the appearances described by Stricker and Norris. Indeed, all the intermediate stages may

* *Loc. cit.*

be readily and completely followed by means of the iodine-absorption method. It is consequently very expedient, besides the researches on corneæ ulcerated with nitrate of silver, or on those which have been caused to inflame by transfixion with a thread, also to institute experiments in which the iodine itself may act as a stimulus to inflammation. The freshly decapitated and entire head of a Frog, after the membrana nictitans has been excised, should be placed with a properly made support in a large iodine chamber, and allowed to remain till the corneæ have assumed their full brown colour, which occupies some hours after the removal of the anterior epithelium. The excised cornea should be examined with the addition of aqueous humour; very remarkable appearances are then presented. The nuclei of the corneal corpuscles will be found to have lost their usual form, and to appear singularly elongated, sinuous, and branched, and withal very smooth and lustrous. Some of the nuclei appear deeply constricted at one point, others have actually broken up into several smaller roundish nuclei. The former obviously coincide with those forms of nuclei that have been described by F. A. Hoffmann* in inflamed corneæ, and which he states resemble migrating cells in all respects, and represent portions of the protoplasm of the stellate cells which have become contractile.

If we place a swathed and living Frog, from which the membranæ nictitantes have been removed, with its head in a vessel containing moistened fragments of iodine, and thus expose the corneæ to the action of iodine vapour, a considerable time usually elapses before the eyes become intensely stained, and the excised corneæ still assume a deeper tint when left in the iodine cell. In the corneæ of Frogs thus treated, the transitional stages between corneal corpuscles and the migratory cells may be very distinctly traced.

In corneæ ulcerated with nitrate of silver, which were examined in large numbers in the iodine cell, the images described by Norris and Stricker were found to be, as already stated, essentially accurate. We see, however, that in corneæ which were as far as possible exposed to the same conditions, very

* *Loc. cit.*, p. 212.

manifold varieties in the inflammatory appearances occur, as Stričker* has pointed out, and, which is a matter of great importance, it may be shown very decisively that in certain cases, at a time when the corneal corpuscles around the ulcerated spot exhibit either very slight indications of proliferation, or none at all, a moderate degree of infiltration of pus may commence from the margin, which may in other cases be entirely absent. In the former case appearances are presented similar to those which have been described and illustrated by Cohnheim in his account of the relations existing between the corneal corpuscles and those of pus.

It is thus placed beyond all question that pus corpuscles can originate from the corneal corpuscles; yet, however satisfactory a proof this constitutes in favour of the protoplasmic nature of the latter, it is equally certain that purulent infiltration of the cornea may occur without the corneal corpuscles in any way participating in the process.

Two sources must be admitted for the migrating cells of the cornea, and unless a given inflammation has been followed through all its stages, from its very first commencement to the particular moment when the changes it produces are subjected to examination, it is not easy to say how many proceed from the one, and how many from the other source, or how many from the fission of previously present migrating cells. †

The origin of the migrating cells present in the healthy non-inflamed cornea from the corneal corpuscles has not been demonstrated. The cells which form the small pustules in keratitis phlyctenularis, which lie between the anterior epithelium and the corneal tissue, and which reach their destination by travelling along the side of the nerves,‡ appear only to be migrating cells that have escaped from the blood.

THE FIBRILLAR SUBSTANCE (FIBRILLAR PORTION OF THE MATRIX) OF THE CORNEA.—The fibrillar substance of the cornea forms the principal portion of its mass.

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* *Studien*, p. 34.

† Stricker, *loc. cit.*, p. 18.

‡ Iwanoff, *Klinische Monatsblatt für Augenheilkunde*, Jahrgang vii., p. 462.

At a time when the cells present in the cornea received but little consideration, though extensive use of the microscope was made, and with very valuable results, for the investigation of animal tissues, the substance of the cornea propria was regarded as a tissue composed simply of fasciculi of fibres.* At a still more remote period a laminated structure was attributed to the cornea, so that according to Haller it is composed of many laminæ.

These laminæ corneæ of the older anatomists have again appeared in the foreground, owing to Todd and Bowman† having described the cornea propria as a "laminated membrane," and recognized the presence of more than sixty lamellæ in the human cornea.

Todd and Bowman, however, described their corneal lamellæ as consisting of a peculiar modification of the white fibrous tissue (fibrillar connective tissue) of the sclerotic, with which the lamellæ are directly continuous. The several lamellæ are further, according to them, so intimately connected with each other by numerous bridges of the same material, that it is impossible to follow any individual lamella beyond a small distance. If now we reflect over this description, the question immediately arises whether the term "laminated membrane" applied to such a structure as that described by Bowman is well applied. Bowman‡ subsequently described the fibrous tissue in a similar manner. Although we find Bowman cited in evidence of the microscopic proof of a lamellated structure of the cornea, and the lamellæ of Bowman are spoken of, the account to which this term may be fairly applied was first given by Henle in 1852, in opposition to his earlier views.§ Thus, according to him, the matter of the cornea is formed by "homogeneous lamellæ," the number of which however (about 300) far exceeds the estimate of Todd and Bowman, but which all run parallel to the surfaces of the corneæ. A further development of the views at that time entertained by Henle will be found in Dornblüth. ||

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* Valentin, *Repertorium der Physiologie*, 1836, p. 311; Donné, *A. Institut*, 1837, No. 220; Henle, *Allgemeine Anatomie*, p. 320 (Leipzig, 1841); Pappenheim, *Specielle Gewebelehre des Auges*, p. 55 (Breslau, 1842); Brücke, *loc. cit.*, p. 9, and others.

† The Physiological Anatomy and Physiology of Man, p. 17. London, 1845 and 1847.

‡ Lectures on the parts concerned in operations on the Eye, p. 10.

§ Canstatt's *Jahresbericht für* 1852, Band i., pp. 26 and 27.

|| Henle and Pfeuffer, *Zeitschrift für rationelle Medicin, N.F.*, Bände vii., p. 212, and viii., p. 156.

Another view of the structure of the cornea was attempted to be established shortly before Henle's later statements, when, in consequence of the doctrines of Virchow on the structure of connective tissue, Reichert's hypothesis on the absence of structure in fibrous connective tissue appeared to obtain an important support from the history of development. This theory of Reichert consisted in the differentiation of the connective-tissue corpuscles from the matrix (fibrillar substance) which he considered to be pure intercellular substance. According to this view, the matrix of the corneal tissue is simply a structureless mass, split up into bands and striæ by the cells deposited in it.* But His† had already again approximated the older doctrines by admitting the existence of corneal lamellæ, which were capable of being separated from each other. In opposition to the two last-mentioned authors, Kölliker‡ strongly supports the fibrous nature of the cornea. Classen§ and Rollett|| also adopt the view of the fibrous structure of the substantia propria corneæ, and more recently Engelmann¶ and Schweigger-Seidel** have done the same. In the meanwhile Langhans,†† under Henle's direction, and Henle‡‡ himself, established the fact that the lamellæ formerly regarded as homogeneous in structure, were composed of extremely fine fibres. In Henle's account, however, we find besides the fact on which he very properly lays stress, of the existence of a laminated structure in the fibrillar substance of the cornea, that he brings too prominently forward the artificial and insufficiently proved distinction between primary and secondary corneal lamellæ.§§

The corneal tissue is now generally regarded as a fibrous structure.

In fact, if a small piece cut from the centre of a fresh cornea be teazed out under water, striated bands or trabeculæ, and

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* Strube, *loc. cit.*

† *Beiträge*, etc., p. 12, *et seq.*

‡ *Mikroskopische Anatomie*, Band ii., Hälfte ii., pp. 608—610, 613—615.

§ *Ueber die Histologie der Hornhaut*, p. 25. Rostock, 1858.

|| *Sitzungsberichte der Wiener Akademie*, Band xxiii., p. 516, 1859.

¶ *Loc. cit.*, pp. 1, 5, and 6.

** *Loc. cit.*, p. 307, *et seq.*

†† *Loc. cit.*, p. 9.

‡‡ *Eingeweidelehre*, p. 595.

§§ *Loc. cit.*, pp. 592 and 593.

slenderer fasciculi, or even separate fibres, are met with, which last are clearly divisions of the former.

The present doctrine of the fibrous structure of the cornea has been arrived at, from its being recognized that the fasciculi and fibres obtained by these mechanical modes of preparation pre-exist. And just as the fasciculi and fibres of the fibrillar connective tissue, so also are those of the cornea isolable, not only by simple mechanical means, but also by means of certain chemical reagents; and in both cases this constitutes the best counter-argument to the objections that have been raised against the pre-existence of the fibrils.

The best means of exhibiting the fibrillation of the corneal tissue is by the application of a solution of permanganate of potash, or of a mixture of this salt and alum,* a fluid that

Fig. 381.

Fig. 381. Fragments of the tissue of the cornea of an Ox, treated with permanganate of potash, and detached from each other by agitation with water. Slightly magnified.

also very beautifully breaks up the fibrillar connective tissue into fibres. Portions of cornea thus treated assume a brown tint, and then break up when shaken with water into longitudinally striated band-like fasciculi (fig. 381), and then again into smaller divisions, and into individual fibrils also running longitudinally.

The disintegrating action of the permanganate of potash

* Rollett, *loc. cit.*, p. 519.

depends on the fact that the fibrils resist destruction longer than the rest of the substance of the cornea, *i.e.* the inter-fibrillar part of the matrix and the cells.

Portions of corneal tissue treated with permanganate of potash do not give any so called Xantho-proteinic acid reaction,* which is not the case with the fresh cornea; this becomes thoroughly yellow on boiling with nitric acid and the addition of ammonium chloride.

Moreover the fibres are rendered easily isolable by macerating sections of the fresh cornea in a ten per cent. solution of common salt,† myosin dissolving out into the solution, from which it can be again obtained by the addition of powdered salt or of water.

Bruns‡ first extracted myosin from the cornea, and attributed its origin to the corneal corpuscles. He therefore believed he had supplied chemical evidence of the contractility of the corneal corpuscles demonstrated by Kühne. Schweigger-Seidel,§ however, owing to his views respecting the corneal cells, is altogether opposed to the idea that the myosin proceeds from them. Kühne‖ states that watery extracts of the cornea contain a large quantity of paraglobulin, which probably proceeds from the corpuscles. A. Schmidt¶ produced coagulation in transudates by the addition of fragments of fresh corneæ. Funke** has demonstrated the presence of albuminate of soda, albumen, and casein, in the watery extract of the cornea. Bruns†† also obtained an albuminate of an alkali from the watery extract of the cornea, and refers the origin of this albuminous body to the fluids permeating the matrix. From what has now been said it is obvious that a knowledge of the distribution of the albuminous substances in the cornea belongs to the category of much wanted but vainly hoped for desiderata. Moreover, it has not been proved that with the

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* Rollett, *loc. cit.*, pp. 523 and 524.

† Schweigger-Seidel, *loc. cit.*, pp. 308 and 352.

‡ *Medicinisch chemische Untersuchungen. Herausgegeben von F. Hoppe-Seyler*, Heft ii., p. 260. Berlin, 1867.

§ *Loc. cit.*, p. 352,

‖ *Lehrbuch der physiologischen Chemie*, p. 386.

¶ Reichert and Dubois' *Archiv*, p. 675, 1861.

** *Lehrbuch der Physiologie*, 2nd Edition, 1858, Band ii., p. 160

†† *Loc. cit.*

albuminous bodies contained in the above-mentioned extracts all is removed that is disintegrated, when, after the addition of permanganate of potash, the so-called Xantho-proteinic acid reaction in the cornea is no longer visible.

The fibrils of the corneal tissue are extremely fine (being at most 0·0001 of a millimeter in thickness), and are arranged in thin ribbon-like fasciculi, the flat surfaces of which in most parts of the cornea either run parallel or nearly parallel to the surfaces of the cornea. In these parts of the cornea the bands lie superimposed on one another in thin laminæ. The direction of the fibrils in the successive layers varies, decussating in various directions, and often completely at right angles (fig. 382). The several layers superimposed upon one another are con-

Fig. 382.

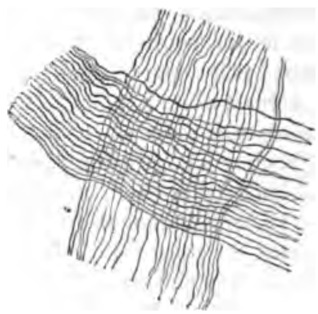

Fig. 382. Two decussating fasciculi of the cornea; from the Ox, treated with permanganate of potash.

nected together by means of fibrils, which pass from one fasciculus to another, and in some places effect a very intimate union between them.

Near the external surface of the cornea, and earlier in some animals than in Man, the fasciculi are inclined towards the free surface, closely interweave with each other, and in vertical sections of the cornea are seen to pursue the most diverse course (fig. 383). The fibres exposed in such sections in their length have, on account of their sinuous course as they pass

* Engelmann, *loc. cit.*, p. 1.

from the deeper to the more superficial layers of the cornea, been incorrectly regarded as something different from the fibrillar substance of the cornea. The so-called supporting fibres (Stützfasern), or fibræ arcuatæ, are nothing but fasciculi of fibrils pursuing this devious course. They may be beautifully seen in sections of corneæ that have been hardened in alcohol of 92 per cent. diluted with its own volume of water.

Such sections made on cork with a very sharp knife, then placed upon a slide, and observed under water, show also that the substance between the fibræ arcuatæ has a finely punctated character.

Fig. 383.

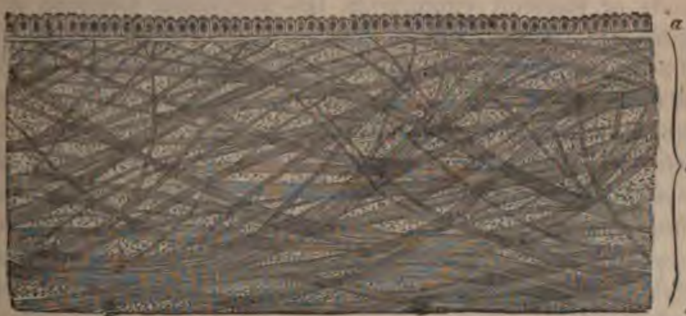

Fig. 383. Section from the cornea of the Ox, hardened in dilute alcohol and immersed in water. *a*, Innermost layer of the anterior epithelium; *b*, external layer of the cornea, with the fibræ arcuatæ (supporting fibres).

This punctation is caused by the transverse section of fibrous bands. In a similar manner we see in sections of the cornea prepared as above the bands of the deeper layers of the tissue divided partly longitudinally and partly transversely; and in the latter case, instead of the striation corresponding to the fibrils, there is likewise a fine punctation. These transversely divided bands appear however to be well defined. They form long thin striæ between the super- and sub-jacent thin longitudinally striated layers, which incline to one another over the pointed ends of the stria corresponding to the transverse sections. In regard to the form of the sections of the bands

of the cornea, Henle * and Schweigger-Seidel † may be consulted.

With crossed Nicol's prisms the transversely divided bands appear dark in all azimuths, whilst the longitudinally and obliquely divided bands appear alternately clear and dark.‡ The optic axes thus coincide with the direction of the fibres.§ The cornea as a whole, when examined as far as possible free from folds, and with its natural curvature preserved, gives, with crossed Nicol's prisms, a dark cross, ‖ which does not alter its position on rotating the membrane around an axis passing perpendicularly to the surface of its vertex (axis of the eye).

This indicates that there is a preponderance of the fibrous bands or fasciculi running in the meridianal direction over those passing in all other directions. If this be correct, the following explanation of the cross may be given. In each of the doubly refracting meridians one plane of polarisation passes through the axis of the cornea (optic axis), whilst the other plane of polarisation is vertical to the latter. Between the crossed Nicol's prisms all those meridians must appear dark whose planes of polarisation coincide with those of the analysers and polarisers, whilst the intervening meridians become brighter in proportion as they are more remote from the dark meridians.¶

We must now consider more closely the layer of the cornea that lies immediately beneath the external epithelium. Its relative thickness in regard to the other layers is shown between b and b' (fig. 377).

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* *Eingeweidelehre*, p. 595, fig. 454.

† *Loc. cit.*, p. 309, figs. 1 and 3.

‡ His, *loc. cit.*, p. 28, *et seq.*

§ Compare Boeck, Taf. ii., fig. 1, and Müller, *Zeitschrift für rationelle Medicin*, 3 Reihe, Band x., p. 173.

‖ Brewster, *Philosophical Transactions*, 1816, p. 315. Valentin, *Untersuchungen der Pflanzen und Thiergewebe in polarisirten Lichte*, (Researches on vegetable and animal tissues in polarised light,) p. 270. Leipzig, 1861.

¶ See v. Lang, *Ueber das Kreuz das gewisse organische Körper in polarisirten Lichte zeigen, etc.*, (On the cross that certain organic bodies exhibit in polarised light,) Poggendorff's *Annalen*, Band cxxiii.

The resemblance of this layer to the membrana Descemetii has already been referred to. It has also been regarded as the analogue of the membrane of Descemet, and as such it has been described by Bowman* under the term, lamina elastica anterior, and by Henle† as the external basement membrane.

The existence of this layer cannot be denied, and it is owing to a misapprehension that Langhans‡ includes me with others who deny its presence.

I have however denied,§ and still continue to deny, that this layer presents the same characters as the membrana Descemetii. The above-mentioned terms therefore are not applicable to it. It may be called by the name that Arnold|| applied to it, of "subepithelial layer of the cornea," or "anterior limiting layer" (Reichert).

This layer breaks up in the cornea of Man and of various animals, after treatment with permanganate of potash, into the same fibrils as the rest of the corneal tissue; whilst the membrana Descemetii, when subjected to the action of the same solution, preserves its capability of rolling inwards, to which we shall hereafter have to refer, its splintery fracture and its structureless aspect.¶ The anterior limiting layer of the corneal tissue is composed of extremely closely interwoven fibrils decussating with each other at all angles. It is not of uniform thickness throughout. It is strongly developed in Man, very

* *Loc. cit.*, p. 5.

† *Loc. cit.*, p. 605.

‡ *Loc. cit.*, p. 19.

§ *Loc. cit.*, pp. 524 and 525.

|| *Die Bindehaut der Hornhaut und der Greisenbogen*, (The connective tissue of the cornea and the arcus senilis.) Heidelberg, 1860.

¶ This layer forms the analogue of that which in the skin is termed the corpus papillare, and has been treated of by Henle as the intermediate skin, by Krause as the superficial layer of the corium, by Bowman as basement membrane or tunica propria cutis, by Kölliker and Gerlach as the superficial layer of the corium, by Virchow as the superficial layer of the corium of the bed of the nail, and by Leydig as the homogeneous limiting membrane of the corium, in regard to which my essay entitled *Untersuchungen über die Struktur des Bindegewebes*, (Researches on the structure of the connective tissue,) *Sitzungsberichte der Wiener Akademie*, Band xxx. p. 50, may be consulted.

slightly developed in the Sheep, Ox, and Pig, and somewhat better again in the Dog and Cat.

After what has been already stated in regard to the structure of the matrix of the cornea, it appears that we cannot speak with propriety of corneal lamellæ. We must, then, describe the smooth fasciculi themselves as lamellæ, which in a certain sense is perfectly correct.

The appearance of a lamellar structure, and the readily demonstrable cleavability of the cornea in a direction parallel to the surface, especially in specimens hardened in dilute alcohol or in Müller's fluid, depends on the superficial arrangement and superimposition of the smooth fibrous fasciculi of the cornea; these, however, are abundantly connected with one another by fibrils running vertically to the surface. Respecting the parts of adjacent superimposed fasciculi not thus connected, but which still undergo the above-mentioned cleavage, an account will hereafter be given.

The fibrils of the cornea, and the fasciculi they compose, swell in water, and become thicker. In acids (acetic acid, pyroligneous acid, and very dilute hydrochloric acid) they also swell up, especially in their transverse diameter; the fibrils and fasciculi thereby become intimately compressed together, their striæ disappear, and the cells become granular, and their intercommunications clearly visible, just as is the case with the cells of connective tissue similarly treated with acids.

In dilute alkalies the corneal fibrils also swell up.

On boiling with water the cornea contracts considerably in diameter, whilst it at the same time becomes much thicker. The fasciculi of fibrils thus behave themselves just like those of connective tissue; and as in this latter case, if sections be made from the cornea and boiled for a short time, and be then dried, when these are again moistened the cells become clearly visible. This plan was formerly much used for the demonstration of the corneal corpuscles.

Both when the tissue has been swollen by immersion in acids and by boiling in water, the fasciculi running through the mass parallel to the surface of the cornea, and which become much thicker transversely—those fasciculi, namely, which bend towards the surface—become stretched and tense, and are

thus mechanically prevented* from thickening and altering like the other fasciculi of fibres of the cornea. They thus produce the peculiar appearance which the so-called fibræ arcuatæ possess in such boiled or acid-swollen specimens, but this does not prove that there is any essential difference between these fibræ arcuatæ and the other fasciculi of the cornea.

If the cornea be boiled continuously, or be heated in an hermetically sealed glass tube, in an oil bath, for a long time, at a temperature of 100° C., a considerable portion of its substance dissolves.

Under this treatment the membrane of Descemet remains for a long period wholly unaltered, whilst even after four or six hours' boiling the fibrillar substance may be completely dissolved, no elastica anterior remaining.†

The liquid filtered from the insoluble residue gelatinizes like solution of gelatine.

The reactions of the fluid are, however, different from those of ordinary solution of gelatine. Johann Müller‡ considered the substance contained in solution to be identical with chondrin from hyaline cartilage. This statement, however, has been denied.

If the corneal gelatine were identical with the chondrin of hyaline cartilage, the chondrin must be obtainable from two different substances; for the fibrillar substance of the cornea has essentially different relations, in regard to water, acids, and alkalies, from the matrix of the hyaline cartilage. In its behaviour with alkalies it agrees far more closely with the fibrils of connective tissue, but it will hereafter be shown to differ essentially from these also.

According to Kühne§ the gelatine from the cornea differs from chondrin only in its non-precipitability with acetate of lead, and the well-marked cloudiness it gives with tannic acid. His|| finds that the corneal gelatine differs from chondrin in

* See A. Rollett, *Berichte der Wiener Akademie*, Band xxx., pp. 60—66.

† See Schweigger-Seidel, *loc. cit.*, p. 355.

‡ Poggendorff's *Annalen*, Band xxxviii., p. 513.

§ *Physiologische Chemie*, p. 386.

|| *Loc. cit.*

re-dissolving in an excess of its precipitants. Bruns,* however, obtained different results in regard to this point, but found that no cartilage sugar (chondroglycose) separates from corneal gelatine when this is heated with hydrochloric acid; on the other hand, he found its specific rotation to the left nearly coincident with that of chondrin. Schweigger-Seidel,† lastly, obtained in one instance, from corneal gelatine from corneæ previously submitted to the action of a ten per cent. solution of common salt, the solution of which however no longer gelatinised, none of the reactions of chondrin; whilst in a second instance, after short duration of the action of the saline solution, he obtained solutions which did do so. Our knowledge of the chemical nature of the fibrillar substance of the cornea and its derivatives is therefore obviously imperfect.

ON THE RELATION OF THE CELLS OF THE CORNEA TO THE MATRIX; INTERFIBRILLAR PORTION OF THE MATRIX AND THE SPACES IN THE LATTER.—Natural cavities in the matrix of the cornea occur only in the form of the serous canals (Saftcanälchen, Hornhauthöhlen) demonstrated by v. Recklinghausen,‡ and these enclose the cells of the cornea.

The serous canals were first examined with precision in corneæ treated with solution of nitrate of silver.

The results of the treatment of the cornea with nitrate of silver, when successful, appear to me to be very satisfactory, if we disregard the chemical changes that are produced.§

Unsuccessful silver preparations cannot however, I think, be held to possess a higher value than unsatisfactory specimens prepared by any other mode of histological research.

Let us commence with the consideration of negative‖ silver preparations. Very beautiful ones may be obtained by immersing the perfectly fresh corneæ of all kinds of animals

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* *Loc. cit.*, p. 263.

† *Loc. cit.*, pp. 355 and 356.

‡ *Die Lymphgefässe*, etc., pp. 36—52.

§ I should not, however, make the same statement in regard to the indications of structure produced by silver in other tissues.

‖ Leber, *loc. cit.*

for a short time—this requiring special testing in each case —in dilute solutions of nitrate of silver containing one part by weight of nitrate of silver dissolved in from 200 to 800 parts of water, and then exposing them in water to the action of light, the rapid action of direct sunlight appearing to be essential for the production of thoroughly successful preparations.

Long exposure to the action of water before examination must be avoided, since this leads to the appearance in silvered preparations of various figures that are difficult to explain.

If the cornea be examined soon after the brown discoloration has thus been quickly produced, white areas are seen in the brown matrix, from which white processes extend in every direction,* the processes anastomose with each other, and, on the whole, appearances are produced which call to mind the protoplasmic plexus of the corneal corpuscles, except that the contour lines of the nodes and processes composing the plexus are more saccular and not so straight as those of the plexus brought into view by treatment with solution of gold. (Compare fig. 384 with fig. 380, *a*.)

The statement of His,† that the figures appearing in silvered corneæ agree in their form with the cells, is under certain circumstances quite correct. It is not, however, always so,‡ because the protoplasm of the cells may wholly or partially detach itself from the walls of the cavities. In view of our own observations on the protoplasmic plexus, rendered visible by placing the cornea in the sinus of the membrana nictitans, or in cells saturated with watery vapour, or in solution of chloride of gold, or by its exposure to the vapour of iodine, we cannot regard as correct the statement that has been made to the effect that, as a general rule, the silver figures do not coincide with the stellate corneal corpuscles, merely because the latter appear with but few branches in specimens examined in aqueous

* His, Virchow's *Archiv*, Band xx., p. 207; and v. Recklinghausen, *loc. cit.*

† *Loc. cit.*, and *Schweizerische Zeitschrift für Heilkunde*, *loc. cit.*

‡ v. Recklinghausen, *loc. cit.*

humour, whilst the silver figures exhibit a closely interwoven plexus.* v. Recklinghausen,† by staining with carmine, has demonstrated in silvered preparations the presence of red scales in these cavities, which sent forth processes into one part of the plexus, whilst another part of the plexus was empty, or only contained small red-coloured and rather lustrous granules. These scales and their processes and the red granules are the remains of the protoplasmic plexus of the cornea, which in silver preparations may be preserved in very different stages of change.

Fig. 384.

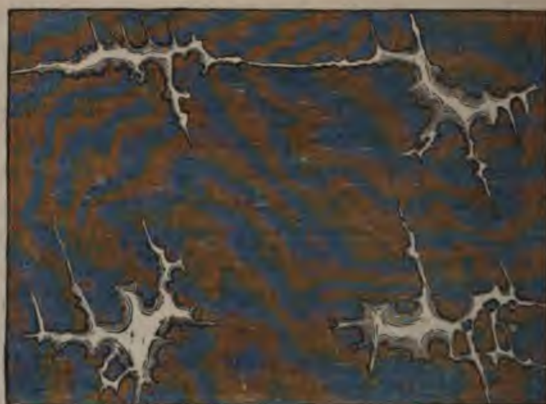

Fig. 384. Preparation taken from the cornea of a Frog, treated with nitrate of silver.

It is of very great importance for the proper understanding of the appearances presented in silver preparations of the cornea, that the successive action of the salt on the tissue should be followed from its very commencement. The best means for this purpose is to treat corneæ silvered in a solution containing one part by weight of nitrate of silver in 200 of water, with a solution of chloride of gold containing 0·5 part by weight in 100 parts of water.

* v. Recklinghausen, see this Manual, Vol. i., p. 314.
† *Die Lymphgefässe*, p. 38.

The brown tint immediately disappears when the specimens are dipped into the latter solution. If, after they have macerated in it as long as when prepared by this means alone, and are then exposed in very diluted acetic acid to the direct action of light, they rapidly acquire a blue colour. This reduction, as may easily be seen under the microscope, is effected by the matrix. And now the same stars and anastomosing processes are seen in the blue matrix as in the silvered specimens, which is essentially due to the fact that the cell substance and nuclei, where these are still preserved, become, by impregnation with the chloride of gold, prominently visible, owing to their distinctly granular aspect and light yellow colour. This may be satisfactorily demonstrated in cases where the nitrate of silver has only acted for a short time, filling these cavities and their processes; for the corneal corpuscles are then distinctly visible in a somewhat swollen condition. If the action of the nitrate of silver has lasted for a longer time, or if the cornea has been too much wasted, which however is to be avoided, the cells and their processes appear still more swollen, and the cavities in the matrix are correspondingly altered. If the silver salt have acted for a still longer period, the cavities in the matrix appear, in the specimens subsequently submitted to the action of gold, empty, and the cells destroyed. We shall hereafter again refer to these preparations. The staining of silvered corneæ by means of logwood is also to be recommended for this purpose, but the results do not surpass those obtained by the combined silver and gold method.

I have already (p. 387) stated that the most remarkable phenomenon accompanying the electrical excitation of the cornea is the apparition of the contour lines of the cavities of the matrix.* The distinctness with which I see this phenomenon, and the unfailing certainty with which I can demonstrate it, render it difficult for me to understand how it has escaped observation.

* A. Rollett, *Ueber die Contractilität der Hornhautkörperchen und die Hornhaut-höhlen*, (On the contractility of the corpuscles and cavities of the cornea,) *Centralblatt für die medicin. Wissenschaften*, 1871, No. 13.

A freshly excised cornea immersed in the aqueous humour of the same eye is made to form a bridge between two platinum electrodes, and is covered with a piece of thin glass, to the margin of which a little fat has been applied. A few opening shocks are then slowly applied, as above mentioned, and very soon the previously homogeneous or only faintly perceptible radiated corpuscles of the cornea make their appearance, and such an appearance as is represented in fig. 385 is seen.

Looped or straight, elliptic, fusiform, or round figures, come into view. The round and elliptic ones have the appearance of sharply defined cavities.

Fig. 385.

Fig. 385. From the cornea of a Frog irritated by means of strong induction shocks (highly magnified).

These clear figures are only the longitudinal, oblique, or transverse sections of the intercommunicating system of cavities traversing the cornea, in the dilated nodal points of which are the nucleated central masses of the radiated corneal corpuscles. This is clearly shown if we try to focus sharply a corneal corpuscle; for it is then seen, as in fig 385, that the finely granular protoplasm of the corpuscle is retracted from the walls of the wider cavity in which it lies, though it still resembles the cavity in its general form, and some attenuated processes from

it may be traced into the processes radiating from the cavity. On the whole, the relation of the protoplasm to the cavities of the matrix is in these cases very similar to that which obtains in many cases of fœtal bone between the bone cavities and the contained cells.

We see, therefore, that in successful specimens obtained by this method, and, as I have said, success is almost constant, the correctness of my statements is confirmed. The appearances in question are best seen with an immersion lens of high power. The irritated corneæ should be quickly treated with iodine vapour, or they may be submitted to the action of gold, and the appearances then presented may be compared with those of the unexcited cornea, and no doubt can be felt in regard to their relations. The cavities of the cornea which are thus rendered visible, cannot be explained by attributing them to any special arrangement or disposition of the fibrillar substance of the cornea alone.

Either there is in the tissue of the cornea a system of canals bounded by a special membrane, from the interior of which the protoplasm can retract, and which either constitutes a distinct entity, or is firmly connected on its exterior with the fibrillar substance, or the cavities of the cornea are imbedded in a substance intermediate to the fibrils and fasciculi of fibrils. The cavities form a plexus with dilated nodal points traversing this substance; and this system of cavities is under certain circumstances completely, under others incompletely filled, by the protoplasmic plexus of the corneal corpuscles.

No membrane answering the former description, and representing a special cell membrane or encysting membrane of the cell plexus of the cornea, can be ascertained to be present either by double contours in optical section, or in the broken and teased-out felt of the ruptured membrane. On the other hand, the appearances presented by the irritated fresh cornea are completely in accordance with the second of the above-mentioned views.

The significance of the appearances seen in silvered and otherwise tinted corneæ—always looking at them from a morphological point of view—presents no difficulties, if we remember simply the three factors of the protoplasmic plexus,

the corneal cavities, and the substance traversed by the fibrils in which the cavities appear to be situated. The chemistry of this subject, and especially of the mode of action of the silver salt, cannot here be entered into in any further detail, and none of the hypotheses respecting it are satisfactory.

The demonstration recently made by Genersich,* that migrating cells may reach and move freely in the interior of the cavities of the cornea when these are rendered distinct by treatment with nitrate of silver, is in accordance with the results of our own observation. In similar accordance with ours are the researches of Hansen,† who found that the corneal cavities underwent changes corresponding with the alterations taking place in the corneal corpuscles in inflammation. Whether at the periphery of the corneal cavities something similar occurs to that which is seen in the lacunæ of bone‡ and in the dentinal tubuli (dentinal sheaths),§ which is supported by some observations, I do not feel myself, from the paucity of my experiments, able to decide, though I regard it as probable.

Injection experiments play an important part in the views entertained upon the structure of the cornea. (See Bowman,|| v. Recklinghausen,¶ Leber,** C. F. Müller,†† Schweigger-Seidel,‡‡ and Boddärt.§§

Boddärt,|||| it appears, was the first who was successful in filling the corneal cavities by puncture injection. Whether

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* *Medicinische Jahrbücher der Gesellschaft der Aerzte in Wien*, Jahrgang 1871, p. 1.

† *Anzeiger der Gesellschaft der Aerzte in Wien*, No. 3, 1871.

‡ See this Manual, Vol. i., p. 124

§ See this Manual, Vol. i., p. 466.

|| Todd and Bowman, Vol. ii., p. 19; Lectures, p. 13.

¶ *Die Lymphgefässe*, etc., p. 41.

** *Monatsblätter für Augenheilkunde*, 1866.

†† Virchow's *Archiv*, Band xli., p. 110.

‡‡ *Loc. cit., et seq.*

§§ *Zur Histologie der Cornea, Centralblatt für die Medicinische Wissenschaften*, 1871, No. 22. This essay has fallen under my notice since this sheet was corrected for the press. It has only caused me to alter the immediately following paragraph. In other respects I must continue to hold my own views.

|||| *Loc. cit.*

this is accomplished by capillary action, as was maintained by v. Wittich* for the formerly admitted intracellular cavities of the corneal plexus, requires, in consequence of the modified views now held, fresh investigation.

The ordinary result of all puncture injections is a rupture of the corneal tissue. These rupture experiments present quite a peculiar distribution of the injected material, in consequence of the regular, but not in all directions equally firm, connection of the fibrous mass constituting the cornea. As a result of this, a series of elongated straight tubular canals (the corneal tubes of Bowman,† intercellular spaces of Henle),‡ or a plexiform system of tubes,§ has been considered to be present in the fresh cornea.

In opposition to the numerous and comprehensive statements made by these authors respecting the injectable spaces of the cornea, it may perhaps be considered that our observations are too concise. This is due, however, to the circumstance that what we are treating of is in reality a very simple matter; the difficulties of the subject have been artificially created, first, through the scarcely conceivable attempt to bring the tubular or pexiform splitting of the cornea into relation with the serous canals (corneal cavities); and secondly, through the perfectly legitimate endeavours to demonstrate lymph spaces in the cornea similar to those which may be so successfully brought into view in other tissues by simple puncture injections.

Various kinds of injection may be applied for the purpose of splitting the cornea. Those with mercury (Bowman) or oily materials succeed better than those with substances in solution or suspended in water (v. Recklinghausen, Leber). The most advantageous one consists of equal quantities of turpentine and olive oil, the latter being coloured with æthereal extract of alkanet. This material should first be employed, and we may readily satisfy ourselves that other modes of injection lead to the same results.

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* Virchow's *Archiv*, Band ix., pp. 90 and 91.

† *Loc. cit.*

‡ *Loc. cit.*, p. 592, fig. 448.

§ v. Recklinghausen, *loc. cit.* C. F. Müller, *loc. cit.* Schweigger-Seidel, *loc. cit.*

Different results, however, are obtained with different animals. In the cornea of the Sheep, Ox, Rabbit, and Frog, we obtain parallel and fasciculated figures, in close juxtaposition to one another, and separated by only very narrow intervals, which run out like spear-heads, and present constrictions of various extent, but rarely communicate transversely. Such fasciculated figures decussating at various angles are superimposed upon one another.

In the Frog, where the injection, although troublesome to effect, yet in some cases succeeds very well, the constrictions in the spear-like figures appear to follow one another quickly, whilst the intervening portions are relatively short. We thus obtain the appearances represented under a low power in fig. 386.

Fig. 386.

Fig. 386. Corneal tubes of the Frog, as seen on injection with an oily fluid.

All injections succeed best in perfectly fresh corneæ, and these should be examined in the aqueous humour immediately after the injection has been made (with Hartnack's objective No. 4, and ocular No. 3, and with gradually increasing powers). If now we compare the appearances obtained by means of injection in the Frog with the silver or gold specimens, and form an unbiassed opinion respecting them, it is difficult to explain why the corneal tubes and serous canals have not always been considered fundamentally distinct things.

But as in Frogs, so is it also in all the above-named animals.

The appearance presented by the injected cornea is, however, different from this in the Dog and Guinea-pig; for here the

injected mass does not form the long spearhead-like figures, but irregularly contoured broad spots, connected with each other by slender bridges. At the periphery of the puncture-injection such spots often appear completely isolated, or are only connected by very slender processes; or they may be joined by broader bridges, and then form an irregular plexus, which is distinguishable from those parts, when the injection is more complete, leaving only small interspaces between the communicating spots by its larger meshes.

In the injected cornea many layers of such plexuses are superimposed one upon the other.

When the plexus presents large meshes, the injection not being complete, figures occur like those that have been depicted by C. F. Müller* and Schweigger-Seidel† in the Dog and Guinea-pig. It is only in certain limited parts, however, that they exhibit exactly the characters that they have illustrated. Whether in such plexuses so regular a distribution of nuclei can be demonstrated by logwood tinting, as C. F. Müller‡ and Schweigger-Seidel§ give, I am unable from my own observation to state. I have never been successful in seeing such images, though it is possible they may be sometimes visible. They are, however, of no special value in enabling an opinion to be formed in respect to the structure of the cornea. The statement made by C. F. Müller,‖ and which may also be deduced from a passage in Schweigger-Seidel's essay,¶ to the effect that in the cornea of the same species of animal elongated lance-like figures come into view in one case, and in another plexuses, according to the force with which the injection is driven, must be called in question. I am certainly of opinion that it is not accurate; for in the first-named animals lance-like shapes are always present, whilst in the Dog and Guinea-pig there are always plexuses.

It is of much greater importance to demonstrate what lesion of continuity has been caused in the corneal tissue by the

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* *Loc. cit.*, fig. 1.
† *Loc. cit.*, figs. 13 and 14.
‡ *Loc. cit.*, fig. 1.
§ *Loc. cit.*, fig. 14.
‖ *Loc. cit.*, p. 138.
¶ *Loc. cit.*, pp. 316 and 317.

injection, than to exhibit by staining the still preserved nuclei of the protoplasmic plexus torn and broken down by means of the injection. This may be very successfully accomplished by extracting the material that has been driven in.

To effect this, the cornea injected in the manner above described should be placed in absolute alcohol. This only colours it slightly, and after a few hours thin horizontal and vertical sections may be made by means of a knife dipped in alcohol. The sections must be placed in æther till the injected fluid has dissolved out, then in alcohol, and finally in water, and examined either immediately or after treatment with staining fluids.

The fibrillar substance of the cornea is then seen to be separated into laminæ, and the fibrillar bands to be laminated, whilst a regular trellis-work of marginal trabeculæ stretches from one to the other with frequent interruptions.

Passing from such fully injected spots to others in which the injection is just commencing to run, every transitional stage from this condition to the more advanced degrees of forcible separation and splitting may be observed. No better illustration of the appearance presented can be given than the comparison of the fibrillar substance of the cornea to a compressed sponge, which has been made by Kölliker.*

If we consider the layers of the cornea forcibly separated by the injection to be so re-applied to one another that all the fasciculi of fibrils resume their original position, the fibrils in such a spongy tissue would be arranged as before, except that in the cornea itself they are attached to each other by means of a cementing material.

We thus believe we have supplied the means by which it may be demonstrated that the ordinary result of simple puncture injections is a forcible separation and breaking down of the tissue of the cornea.

That the meshwork resulting from the forcible separation presents different characters in different animals shows that the fibrils do not pursue the same course in all.

Schweigger-Seidel† makes the forcible separation of the

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* *Mikroskopische Anatomie*, Band ii., 2te Hälfte, p. 610.

† *Loc. cit.*, p. 321.

cornea available for the demonstration of his nucleated plates or laminæ. How these come to be isolated will be considered hereafter.

We must now refer to the, as already stated, not certainly proved system of canals lined with flattened cells, which Hoyer* obtained by the silver method of preparation in that layer of the corneal tissue of the Kitten, which is in immediate relation to the membrana Descemetii; which C. F. Müller † states he has seen in all the layers of the cornea in two embryoes of the Cow, having a length of thirty-eight and forty-one millimeters, as well as in the Dog, Pig, and other animals, and which, lastly, Schweigger-Seidel‡ mentions, and has drawn as it is seen in the Dog.

This appearance I am well acquainted with, but I find it only in young animals, and only well marked in the layers close to the membrane of Descemet, as may be demonstrated in any small Rabbit.

Broad silver spaces, bulging at intervals, which are continuous with each other by means of broad bridges, exhibit in their interior sharply defined black lines, by which the silver spaces are divided into areas having the same appearance as endothelial or epithelial cells when bounded by a silver marking. The black lines correspond to actual cell boundaries. The cells which meet in these lines are not plates, however, but corneal cells, between which no fibrillar matrix, or but a very sparing amount of it, is developed.

The whole of the cornea at a certain period of development consists of just such closely compressed and originally roundish cells, and their development into corneal tissue proceeds from the anterior towards the posterior surface of the cornea. In young animals the same contour lines are presented in the layers on the membrane of Descemet, which, during the development of the cornea, are met with in all the other layers; and we there obtain the silver image described by Hoyer, as has been stated by C. F. Müller for the embryo of the Cow, and as I have also observed in the embryoes of Sheep.

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* Reichert and Dubois-Reymond's *Archiv*, 1865, p. 214.

† *Loc. cit.*, p. 132.

‡ *Loc. cit.*, fig. 16.

I am unable, on account of the insufficient number of my investigations, to give the limits of age at which in a given animal the contour lines are still preserved in the layers immediately adjoining the membrane of Descemet, and when these can no longer be seen. It is, however, certain that the markings are not visible in the fully developed cornea of adult animals

Great care should be taken in the investigation of specimens too long exposed to the action of water, or of silver preparations that have become distorted, or decayed, or broken down, in all of which illusory appearances of the most various kind may occur. The appearances described by Hoyer are thus explained by the progress of the development of the cornea, and are as little in favour of the existence of cavities lined with flattened epithelial cells as the rupture of the cornea by puncture injections.

A few observations must still be made on that part of the matrix of the cornea in which we consider the corneal cavities with their processes to be imbedded (interfibrillar part of the matrix). Very little is known respecting the nature and peculiarities of this substance; we must, however, regard it as a continuously connected portion of the cornea, distributed through it in a definite but not uniform manner. Its distribution is primarily dependent upon the arrangement of the fibrils and fasciculi of fibrils. If we conceive this interfibrillar substance to be rigid and the fibrils to be removed, and if we further imagine the protoplasmic network extracted from the corneal cavities, the skeleton that would remain would consist of this substance.

This skeleton, however, has perfectly definite morphological characters. If a vertical section be made with a sharp knife through a perfectly fresh cornea resting upon a piece of cork, and the two surfaces of the section be separated from one another under water, we shall see numerous elongated cavities; and where these spaces (the interlamellar cavities of Henle) exist, the fasciculi of fibrils are in less intimate contact than in the bands of tissue which occupy the interstices between the spaces. The cavities are occupied by the flat bodies of the corneal corpuscles. But if we compare the length of the

spaces with the length of the flat middle portion of the corneal corpuscles, we shall find that the former are much larger than the latter. There must therefore be deposited within and around the cavities containing the corpuscles and separating the fasciculi from each other, a broad thin layer of that substance extended parallel to the corneal surface, whilst it occurs also finely divided in the smaller passages between the fibrils, and around the processes of the corneal corpuscles running in the direction from one surface of the cornea to the other (fig. 380, *b*). In coincidence with the peculiar arrangement and distribution of the corneal corpuscles and the fasciculi of fibrils (compare figs. 377 and 380, *b*), these large flat layers of intermediate substance run in general in the direction of the corneal surfaces, and, being inclined towards each other, coalesce and are connected by variously formed laminæ and striæ.

Specimens may also be prepared by teasing out the tissue of the above-mentioned (p. 404) corneæ, which have been first silvered, and then subjected to the action of gold. The several fasciculi of fibrils then frequently exhibit the indication of the contours of the still uninjured or, owing to the effect of the needles, disrupted corneal cavities. The fibrils themselves, where they have become completely isolated, are smooth, and are either not at all, or only feebly, stained. The blue colour adheres to a mass which appears to be traversed by the fibrils; this mass seems to be beset with granules, and thus, as it on the one hand surrounds the fibrils, so does it form on the other the proper walls of the cavities.

The above-mentioned skeleton of cementing substance can be isolated from the fibrils of the cornea, though in a distorted, variously torn, and collapsed condition, and this may be accomplished by converting the corneal fibrils into gelatine by prolonged boiling in water or in alcohol acidulated with hydrochloric acid (strong alcohol, containing from 0·5 to 0·75 per cent. of fuming hydrochloric acid).

In the cornea of the Ox, Dog, and Sheep, no other change is observable besides the already mentioned sudden alteration of form which occurs immediately on boiling the cornea with the acidulated alcohol. The corneal fragment, however, becomes progressively freed from the soluble gelatine-yielding

substance, and exhibits (as is shown in vertical sections prepared at different times) that appearance which in boiled sections of the cornea has been described as the expression of the lamellar structure of the cornea; it ultimately splits up very easily into leaves and leaflets. Lustrous striæ, here and there thickened, and in parts inclined towards one another, are superimposed in many layers in the direction of the thickness of the membrane.* When Schweigger-Seidel † states that by the aid of acidulated alcohol he has succeeded in bringing coincidently into view the transparent glass-like scales of his corneal cells, as well as the lustrous granular striated corpuscles (artificially made, Schweigger-Seidel) in immediate contact with them, he is speaking of the flat middle portion of the corneal corpuscles, surrounded by some still adhering cement. A similar explanation must also be given of the laminæ, or scales, which may be isolated by driving fluid injection into the cornea.

In regard to the paths pursued by the migrating cells of the cornea, we must, in accordance with the account above given, explain that they are to be sought in the system of canals filled by the soft protoplasmic plexus of the corneal corpuscles (v. Recklinghausen). The presence of a fluid substance, uniformly distributed through the cornea in which the solid

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* In the above account we have limited ourselves to our own observations upon this substance. It is, however, partially at least, supported by what Lightbody, unfortunately without specifying his mode of preparation, has stated in his paper "On the Anatomy of the Cornea of Vertebrates," (*Journal of Anatomy and Physiology*, Vol. i., 1867, p. 16.) "The fasciculi," he says, "are connected to each other by a gelatinous form of connective tissue, which varies greatly in quantity and consistence in different animals. In the Rabbit it is abundant and hard; in the Rat it is also abundant, but so soft, especially near the margin of the cornea, that if the conjunctival epithelium be scraped off rather roughly it is squeezed out of place, and presents much the same aspect as Bowman's corneal tubes, which I believe are generally considered to be an artificial separation of the bundles. This gelatinous substance is tinted by carmine, though not so deeply as the corpuscles and their processes which lie imbedded in it, yet more deeply than the tissue composing the bundles; this last is hardly stained at all, unless the solution of carmine is very strong, and what it does absorb then is tolerably easy to wash out."

† *Loc. cit.*, p. 323.

morphological elements float, and in which the migrating cells, pushing aside these morphological elements, can pursue their destined path* is not in accordance with the phenomena observed. It must be left for future researches to decide whether transuded fluids cause, or are capable of causing, forcible separation of the corneal tissue, like that produced by puncture injections, and whether in such transudates formed elements resembling amœboid cells are present.

THE VESSELS OF THE CORNEA.—The central portion of the cornea in adult vertebrate animals is destitute of bloodvessels.

In Man there is only a marginal zone of delicate capillary loops, with a diameter of from one to one and a half millimeters. These arise from the arteries running in the outer layer of the most anterior part of the conjunctiva bulbi, and discharge themselves into the subjacent veins of the same membrane (fig 387).

For the origin of these arteries, and the mode of formation of the veins, the reader is referred to the chapter in this Manual on the "Bloodvessels of the Eye."

According to Leber, in the eye of Man there are no deeper-lying vessels entering the deeper parts of the cornea from the sclerotic.

In Man, after death, the vascular loops at the margin of the cornea may frequently be seen very beautifully injected naturally. As a rule, elongated and wide-meshed loops may be seen naturally injected in the perfectly fresh eye of the Sheep.

In the eye of the fœtus a delicate capillary plexus is distributed over the whole of that layer of the anterior surface of the cornea on which the anterior epithelium rests.

Isolated and doubtful observations have been made by Kölliker,† His,‡ and Sämisch,§ respecting the presence of lymphatics at the margin of the cornea. The statements of

* Engelmann, *loc. cit.*, p. 6, *et seq.*

† *Mikroskopische Anatomie*, Band ii., p. 621.

‡ *Beiträge zur normalen und pathologischen Histologie der Cornea*, p. 71.

§ *Beiträge zur normalen und pathologischen Anatomie des Auges*, p. 12. Leipzig, 1862.

Lightbody,[*] to the effect that perivascular lymph spaces surround the marginal loops of the cornea, have not been corroborated as a normal condition by C. F. Müller [†] or by Schwalbe.[‡] Neither C. F. Müller [§] nor Schweigger-Seidel [||] were successful in discovering any mode of exit for the fluid driven into the substance of the cornea by puncture-injections; but Leber[¶] has observed the entrance of injected fluids into the lymphatics of the conjunctiva.

Lastly, it may here be observed that in simple puncture-injections into the cornea, the injected fluid may make its way along the trunks of the nerves,[**] and this may also occur from the extravasation of injection fluids driven into the bloodvessels. In this way are to be explained, according to C. F. Müller,[††] the vascular-like figures observed by Teichmann in the injected cornea,[‡‡] and the vasa serosa described by J. Arnold [§§] and by Niemetschek.[||||]

THE MEMBRANE OF DESCEMET.

The membrane of Descemet forms a very sharply defined layer in vertical sections of the cornea; its thickness increases in Man with the advance of years. In the newly born child H. Müller[¶¶] found its thickness to amount to 0·005—0·007 of a millimeter; in the adult and at the centre, to 0·006—0·008 of a millimeter; at the margin, from 0·01 to 0·012 of a millimeter; in old people, in the centre, to 0·01; and at the margin, to 0·015—0·02 of a millimeter. It is detached with difficulty from the fresh cornea, but with facility from a cornea treated with permanganate of potash, or with a ten per cent. solution of common salt.

* *Journal of Anatomy and Physiology*, 1867, p. 35, *et seq.*

† C. F. Müller, *loc. cit.*, p. 147.

‡ *Archiv für Mikroskopische Anatomie*, Band vi., p. 264.

§ C. F. Müller, *loc. cit.*, p. 146.

|| Schweigger-Seidel, *loc. cit.*, pp. 324 and 325.

¶ *Klinische Monatsblätter für Augenheilkunde*, 1866, p. 17.

** C. F. Müller, *loc. cit.*, p. 142.

†† C. F. Müller, *loc. cit.*

‡‡ Teichmann, *Das Saugadersystem.*

§§ J. Arnold, *loc. cit.*

|||| *Prager Vierteljahresschrift*, Band iii., 1864, p. 48.

¶¶ *Archiv für Ophthalmologie*, Band ii., Abtheil. ii., p. 48.

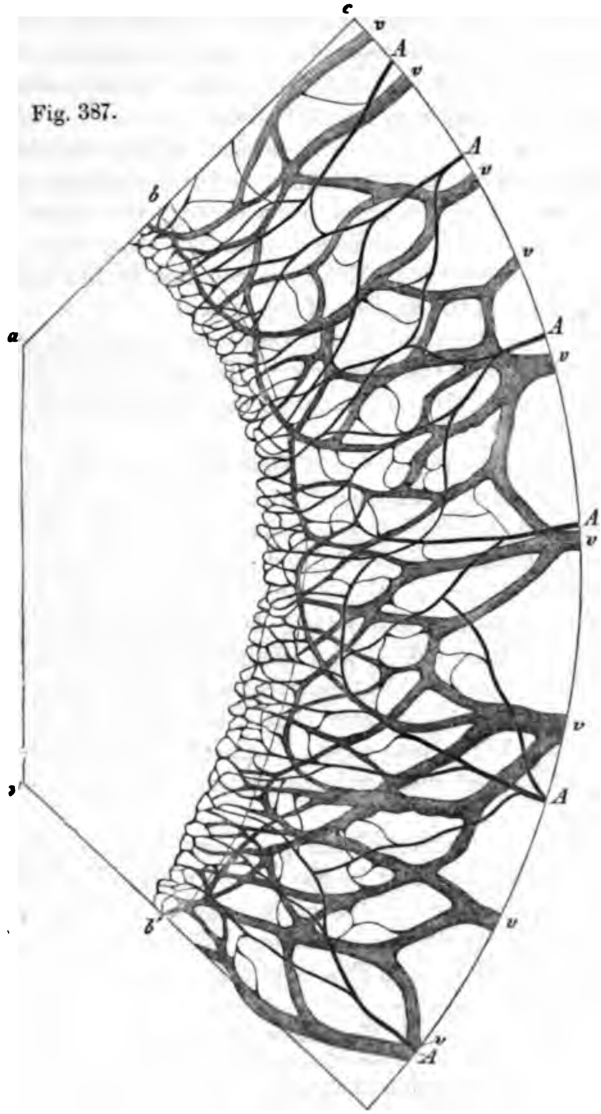

Fig. 387. Terminal loops, *b b'*, proceeding from the most anterior conjunctival vessels ; *A*, arteries ; *v*, veins ; *a a' b b'*, *cornea; b b' c c'*, conjunctiva and sclerotic. Drawing taken from the eye of a child, very perfectly injected with gelatine and Prussian blue.

Portions of the membrane detached either from the fresh cornea or from a cornea treated in the above-mentioned manner are characterized by the rolling inwards of the opposite edges, like paper that has been long rolled up.

The borders of a detached portion of the membrane of Descemet are very sharply defined under the microscope; and as, on account of its great transparency, the foreshortened image of all angles is visible, a glass-like appearance is produced. All these peculiarities are common to the membrane of Descemet and the capusle of the lens.

When fresh, the membrane of Descemet presents no structure recognizable under the microscope. In rare instances only an indistinct and interrupted striation may be perceived on fractured surfaces.*

Henle† saw the membrane of Descemet of the eye of the Ox, after thirty hours' boiling, break up into a number of extremely fine, somewhat inrolled, glass-like laminæ. Tamamscheff‡ noticed that fine sections of dried corneæ, when submitted for twenty-four hours to the action of solution of iodide of potassium containing iodine (3 : 1 : 500), become striated in the direction of the surface, and divisible into extremely fine fibrils. Schweigger-Seidel§ describes and depicts some peculiar appearances, and also states that a ten per cent. solution of common salt brings into view a distinctly fibrillar striation in the membrane, but whether in the superficial or side view is not specified.

Wart-like projections of the posterior surface of the membrane of Descemet occur in Man at the margin of the cornea.‖ These are not present in the early years of life, but between twenty and thirty they have a diameter of 0·01 of a millimeter at their base, are about half this height, and stand in from two to

* Brücke, *loc. cit.*, p. 606. Mensonides, *Nederlandisch Lancet*, Mai, 1849, p. 694. Leydig, *Zeitschrift für wissenschaftliche Zoologie*, Band v., p. 41.

† Canstatt's *Jahresbericht*, 1853, p. 26, and *loc. cit.*, p. 606.

‡ *Centralblatt für die medicin. Wissenschaften*, 1869, p. 353.

§ Schweigger-Seidel, *loc. cit.*, pp. 311 and 312, figs. 7, 8, 9, and 10.

‖ Hassall, *Mikroskopische Anatomie*, translated into German by Kohlschütter, Band ii., Taf. lxiii., fig. 11, p. 393. Leipzig, 1852. H. Müller, *Archiv für Ophthalmologie*, Band ii., Abtheil. ii., p. 48.

four rows, at distances from each other that are about equal to the diameter of their bases. In old people they are about 0·02 of a millimeter wide at their base, and 0·01 of a millimeter high, and form a broad zone. In rare cases they extend as far as the centre of the cornea (H. Müller).

The connections formed by the membrane of Descemet at its border will be subsequently considered.

The Endothelium of the Membrane of Descemet.

Internal Epithelium of the Cornea.

The endothelium of the membrane of Descemet consists, in the eye of Man and of adult animals, of a layer of polygonal cells, having a diameter of 0·025 of a millimeter.* The cells have a flattened appearance, and possess round nuclei, with a diameter of 0·008 of a millimeter.† In perfectly fresh eyes the endothelium may be stripped off in the form of a continuous membrane. This layer of cells situated at the back of the cornea is not to be included amongst the true epithelia, but amongst the endothelia.‡

In the endothelial cells of the membrane of Descemet of the irritated cornea of the Frog, Klebs§ observed the occurrence of a series of alterations of form, which under certain circumstances are as lively as those of the lymph corpuscles, and lead to detachment of the cells. Norris and Stricker‖ also saw movements take place in the endothelial cells of the membrane of Descemet in inflamed corneæ, and state that they observed an increase in the number of the nuclei, and a proliferation of the cells. If the freshly excised and healthy cornea of the Frog be moistened with aqueous humour as rapidly as possible, be brought under the microscope, and the endothelium of the membrane of Descemet be examined whilst in accurate focus, it will frequently appear as if composed of two kinds of

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* Henle, *loc. cit.*, p. 607.

† Henle, *loc. cit.*

‡ His, *Häute und Höhlen des Körpers* (Membranes and cavities of the body), p. 18. Basel, 1865.

§ *Centralblatt für die medicin. Wissenschaften*, 1864, pp. 513—516.

‖ Norris and Stricker, *loc. cit.*, pp. 16 and 17.

cells. Some of the cells appear granular, and contain a round nucleus with a more or less well-defined contour; whilst others, on the other hand, appear perfectly smooth and without any indication of a nucleus. These two kinds of cells either occur isolated or connected together into irregular figures, the variations in the distribution of the two occasioning very diverse markings of the endothelial membrane.

Development of the Corneal Layers belonging to the Connective Tissue.

The histogenesis of the cornea requires to be again worked over, especially with the aid of the silver and gold methods of preparation. At present our knowledge of this subject is very fragmentary. Langhans* found in the cornea of the fœtus of a cow, one inch and a quarter long, elongated and roundish cells, with not very sharply defined nuclei, lying in close apposition. In an embryo with a length of one inch and a half, the cells were irregularly roundish or angular in form. In an embryo two inches and a half long, a fibrous appearance was already visible in the teazed-out tissue; the cells were large, and their form resembled more closely the corpuscles of the developed cornea. In the fœtus of a Cow, the diameter of the eye of which amounted to about 0·6 of a millimeter, the cells were pale, elongated, and had from four to six processes.

I have in my possession a series of meridianal sections of the embryoes of Sheep hardened in Müller's fluid, tinted with carmine, and imbedded in Peremeschko's solidifying mass. In these I can see that the cornea is originally composed of round cells in immediate contact with each other. Subsequently the cells appear to be flattened towards the surface of the cornea and lie superimposed one upon the other, like the cells in the upper layers of laminated tesselated epithelium.

A clear substance intervenes between these flattened cells, separating them from each other in the direction of the thickness of the cornea, so that appearances are already produced resembling those of the fully developed cornea.

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* *Loc. cit.*, pp. 17 and 18.

This separation of the cells from one another does not occur uniformly in all the layers of the cornea. It commences near the anterior pole of the eye, affects the anterior layers first, and then extends progressively backwards towards the anterior chamber.

At a certain period of development this layer is separated from the corneal layer with already fully developed intermediate substance by a layer of flattened cells superimposed one upon another, the innermost of which exactly resemble the cell layer corresponding to the endothelium of the membrane of Descemet. The membrane of Descemet is not as yet present. It occurs as a slender stria between the innermost cell layer and the cells forming plates superimposed one upon the other situated more externally.

In the embryo of a Calf eight centimeters long, and in human embryoes of the second or third month, the membrane of Descemet presents, according to Donders,* the same structureless appearance as in adult animals, except that it is thinner.

In the clear substance which, as mentioned above, separates the flattened cells of the developing tissue of the cornea, fine fibrils or fasciculi of fibrils occur at a very early period. The cells themselves appear to be provided with processes which radiate from them in all directions, and anastomose with the processes of neighbouring cells, but which, as is shown by teazed-out preparation and by sections, are never continuous with the substance of the fibrils.† The latter occur in the material occupying the interspaces of the granular protoplasm of the cells, in the same manner as the fibrils of the connective tissue in the development of the plexus.‡ The histological processes taking place in the cornea of Rabbits after the anterior layers have been shaved off,§ and in the cornea of Man

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* *Nederlandisch Lancet*, August, 1851, p. 47.

† See Wilckens, *Ueber die Entwicklung der Hornhaut des Wirbelthier-auges*, (On the development of the cornea of the eye of vertebrate animals,) *Zeitschrift für rationel. Medicin*, 3 R., Band xi., p. 167.

‡ See this Manual, Vol. i., p. 84.

§ Donders, *Holländische Beiträge zur Natur- und Heilkunde*, Band i p. 387. De Gouvea, *Archiv für Augen- und Ohren-heilkunde*, Band p. 119.

after losses of substance,* and the regeneration of the tissue which has been observed to occur, likewise demand a more profound and searching investigation.

THE EXTERNAL EPITHELIUM OF THE CORNEA.

This epithelium is a laminated pavement epithelium, which in Man is 0·03 of a millimeter in thickness.† The characters of the external epithelium are very much alike in Man and Mammals.

Its most superficial layers are composed of many layers of flattened cells, which are broader than those that are more deeply situated, and which, seen *in situ*, as in sections of hardened preparations, or in detached shreds of the epithelium,

Fig. 388.

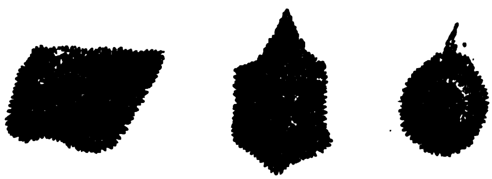

Fig. 388. Ribbed and spinous cells from the middle cell layer of the external corneal epithelium of the Pig, isolated by maceration of the cornea in a ten per cent. solution of common salt, and subsequent treatment with water.

present a polygonal form. In teazed-out specimens of epithelium prepared in iodine-serum, or for a longer period in a ten per cent. solution of common salt, and subsequently for a short time in water, these cells appear rough, slightly dentated, and as ribbed, spiny, or prickle cells, with their inequalities interlocking with each other (fig. 388). I have never been able to see any cells provided with such long processes (digitate cells) as Cleland‡ states that he has isolated from the middle layers of

* Donders, *Nederlandisch Lancet*, 1848, p. 218.

† Henle, *loc. cit.*, p. 605.

‡ Cleland, On the Epithelium of the Ox, *Journal of Anatomy and Physiology*, by Humphry and Turner, Vol. ii., pp. 362, 364. Cambridge and London, 1868.

the corneal epithelium of the Ox by means of the bichromate of potash, and which he has depicted.

The deepest cell layer resting directly on the corneal tissue is composed of cells that are vertically elongated. They are isolated, but rough in consequence of their detachment from the interdentations of the adjoining ones, and are seated with their broad bases upon the corneal tissue. They do not send off any processes into this. When seen in profile, the base of the cells appears as a highly refractile line (basal hem or border). The round nucleus of these cells is somewhat nearer their outer than their inner extremity. It may be particularly well seen in sections stained with hæmatoxylin, and rapidly hardened in alcohol, of the cornea of those animals that possess remarkably long cells, as for example in the Ox and Pig. Krause* states he has observed peculiar ellipsoidal cells to be sparingly distributed amongst the cells of these layers.

In the Frog, the epithelium as seen in optical section, where the fresh cornea has fallen into folds, presents the appearances presented in fig. 378.

I have convinced myself that here also maceration in a ten per cent. solution of common salt until the epithelium separates in shreds,† constitutes an excellent means of isolation.

The cells of the outermost layers form a kind of mosaic, the areas of which are circumscribed by highly refractile branching lines (cell contours with cement that blackens with nitrate of silver), and every polygonal cell contains a beautiful sharply defined granular nucleus (fig. 389, *a*).

Rib and prickle cells occur sparingly in the middle cell layers of the Frog. The cells there appear either polyhedric with smooth borders and surfaces, or, as may frequently be observed, they give off a limited number of longer or shorter pointed, and often very peculiarly formed, processes (fig. 389, *b*).

The innermost cell layer is here also composed of elongated cells, which, however, vary in length. Thus between shorter

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* *Ueber das vordere Epithel der Cornea*, (On the anterior epithelium of the cornea,) *Göttinger gelehrte Nachrichten*, 1870, No. 8; Reichert and Dubois-Reymond's *Archiv*, 1870, p. 232.

† Schweigger-Seidel, *loc. cit.*, p. 353.

cells of the form represented at *c* 1, fig. 389, longer ones are intercalated of the form seen in *c* 2, fig. 389, and the clavate form of cell may often be seen still more strongly expressed on account of the attenuation of the inner part of the cell, as in *c* 3, fig. 389.

A highly refractile hem or border (fig. 389, *c* 1 2 3) exists at the point where the cells rest upon the corneal tissue, which in

Fig. 389.

Fig. 389. External epithelium of the cornea of the Frog. *a*, Cells from the outermost, *b*, from the middle, and *c*, from the innermost layer.

profile views recalls the smooth border that under some circumstances certain columnar epithelial cells exhibit at their free margin. This border, which may be termed the basal border, usually appears to be expanded, and this is always the case with the clavate cells of the innermost layers.

The expanded basal borders of the cells are so applied to each other, or are so superimposed upon one another by their thin edges, that the borders of the several cells seen collectively *in situ* make a bright stria which forms the line of demarcation between the epithelium and the corneal tissue. Henle* mentions this stria, but gives another interpretation of it.

I have satisfied myself, as regards Man and Mammals, that the stria is due to the basal borders of the innermost cells.

An accurate knowledge of the normal condition of the different layers of the corneal epithelium is so much the more requisite, as this epithelium plays an important rôle in the investigations that have recently been made in regard to epithelial regeneration.

J. Arnold,† who began the investigation, it is well known advanced a proposition of quite fundamental importance in admitting that the new epithelium filling an artificially produced abrasion of the epithelium arises from a blastema formed in the hollow. This, he thought, became converted at the border of the space into hyaline protoplasm, which divides into portions containing nuclei, *i.e.* into cells. The experiments on the external epithelium of the cornea made by Wadsworth and Eberth,‡ F. A. Hoffman§ and Heiberg,‖ are however collectively opposed to the existence of Arnold's blastema. The regeneration occurs through the agency of daughter cells that arise by germination and fission of the epithelial cells forming the border of the cavity, or from the marginal cells of epithelial islands remaining intact in the cavity.

F. A. Hoffman¶ states that he never observed processes in the cells of the lowermost epithelial layers. This would indicate that the last-named layer had a definite position (see Cleland** and Krause).†† Heiberg,‡‡ however, opposes Hoffman's statements. But Heiberg lays too little stress on the peculiarity of the intact lowermost cell layer of the

* Henle, *loc. cit.*, p. 605, fig. 459.

† Virchow's *Archiv*, Band xlvi., p. 168.

‡ Virchow's *Archiv*, Band li., p. 361.

§ Virchow's *Archiv*, Band li., p. 373.

‖ *Medicinische Jahrbücher der Gesellschaft der Aerzte in Wien*, Jahrgang, 1871, p. 7.

¶ Hoffman, *loc. cit.*, pp. 388 and 389.

** Cleland, *loc. cit.*, p. 363.

†† Krause, *loc. cit.*, p. 235.

‡‡ Heiberg, *loc. cit.*, p. 19.

corneal epithelium. We have already seen that processes are present even in the normal condition in the cells of the middle layers. Heiberg* describes slow and gradual changes of form in the processes of the epithelium undergoing regeneration. F. A. Hoffman† had previously observed the protrusion and retraction of rounded processes in the cells of the anterior corneal epithelium in the vicinity of the eschar of the cornea caused by nitrate of silver. The regeneration of the epithelium in a cavity (the size of which is unfortunately not stated) caused by scratching the centre of the surface of the cornea with a cataract needle is accomplished in Frogs in about forty hours, or as a rule before the end of the third day, and in Mammals and Birds within twenty-four hours. After these periods had elapsed, the cavities were found to be completely filled up by cicatrisation.‡

Migrating cells occur in the anterior corneal epithelium, just as in the corneal tissue, and such cells are also found between the two tissues (epithelial and subepithelial migrating cells).§ Engelmann,|| J. Arnold,¶ Wadsworth and Eberth,** F. A. Hoffman,†† and Heiberg,‡‡ consider it doubtful whether the migrating cells take any part in the regeneration of the epithelium after losses of its substance.

The Nerves of the Cornea.

The nerves of the cornea enter its margin at tolerably regular distances from each other in the form of trunks of various size. The entrance of medullated nerves into the cornea has long been known to occur.§§

The number of such medullated nerves entering the cornea

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* *Loc. cit.*, p. 12.

† *Ueber Contractilitätsvorgänge im vorderen Epithel der Froschhornhaut. Diss. inaug.* Berlin, 1861.

‡ Heiberg, *loc. cit.*, p. 10.

§ v. Recklinghausen, Virchow's *Archiv*, Band xxviii., p. 191.

|| Engelmann, *loc. cit.*, p. 15.

¶ J. Arnold, *loc. cit.*, p. 170, *et seq.*

** Wadsworth and Eberth, *loc. cit.*, p. 370.

†† F. A. Hoffman, *loc. cit.*, p. 384.

‡‡ Heiberg, *loc. cit.*, pp. 13 and 20.

§§ Schlemm, *Berliner Encyclopädie*, Band iv., p. 22. Bochdalek, *Bericht über die Versammlung der Naturforscher in Prag im Jahr.*, 1837, Prag, 1838, p. 182.

varies in different animals. In Man the number is variously stated at from twenty to thirty,* twenty-four to thirty-six,† and forty to forty-five.‡ In the Rabbit, from twenty to thirty; in the Ox and Sheep, from ten to twenty; in the Fowl and Pigeon, from twelve to eighteen;§ in the Guinea-pig, from fifteen to eighteen;|| and in the Frog, on the average, fifteen¶ have been counted. In the course of their distribution in the substance of the cornea, the nerves form a plexus characterized by its numerous anastomoses, the fine branches of which run towards the anterior surface, where another plexus is found close beneath the epithelium, and just under the anterior structureless lamella.** The nerve plexus formed of non-medullated fibres presents the same appearance in Man and the most diverse animals,†† and in the Frog the fine extremities of the nerves distributed through the whole cornea are connected with the corneal corpuscles.‡‡

In Mammals, the fibres emanating from the outer parts of the nerve plexus may be followed into the anterior epithelium of the cornea.§§ The best insight into the mode of distribution and the termination of the nerves in the cornea, has been obtained by Cohnheim,|||| by the use of solution of chloride of gold, which is so admirably adapted for this purpose. His beautiful results have been in part corroborated both by Kölliker and by Engelmann.

At a short distance from the margin of the cornea, the

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* Kölliker, *Mikroskopische Anatomie*, Band ii., p. 627.

† Kölliker, *Gewebelehre*, p. 650. Leipzig, 1867.

‡ Sämisch, *Beiträge zur normalen und pathologischen Anatomie des Auges.*

§ Kölliker, *Mikroskopische Anatomie*, Band ii., p. 627.

|| Cohnheim, Virchow's *Archiv*, Band xxxviii., p. 354.

¶ Kühne, *Untersuchungen über das Protoplasma*, etc., p. 133. Leipzig, 1864.

** Kölliker, *loc. cit.*, p. 627.

†† His, *Beiträge zur normalen und pathologischen Anatomie der Cornea*, p. 60. J. Arnold, *Bindehaut der Hornhaut*. Sämisch, *loc. cit.* Ciaccio, *Quarterly Journal of Microscopical Science*, July, 1863, p. 177. Kühne, *loc. cit.*

‡‡ Kühne, *loc. cit.*

§§ Hoyer, Reichert and Dubois-Reymond's *Archiv*, 1866, p. 180.

|||| Cohnheim, *loc. cit.*, p. 343.

medullated nerve fibres suddenly lose their medullary sheath. The point at which this occurs is not constant (Cohnheim), sometimes occurring in the small entering trunklets, sometimes in the branches of the first, second, or even the third order into which these break up.

The nerves in their further course from this point are composed of a variable, but usually very large, number of extremely delicate non-medullated nerve fibres. These fasciculi of non-medullated fibres enclose long oval nuclei, which cannot, however, be certainly shown to belong to any investing sheath.

Fig. 390.

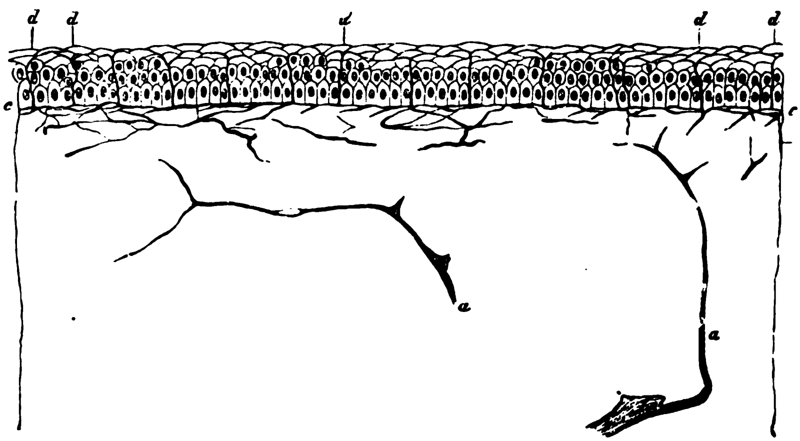

Fig. 390. Nerves of the cornea of a Pig, as seen in a vertical section made from a specimen treated with chloride of gold. *a a*, Larger nerves ; *b b*, plexus beneath the anterior limiting layers of the cornea ; *c c*, subepithelial plexus ; *d d*, the terminal branches ascending through the epithelium.

The individual medullated fibres often exhibit a very beautiful varicose appearance. These numerous fibres must obviously originate in a division or fibrillation of the axis cylinder (Max Schultze).

The fibres just described as entering the corneal tissue then form, by their manifold branching, communications, and divergences, a rich plexus (fig. 390), which presents larger meshes, and is composed of stronger nerves in the deeper part of the

cornea, whilst towards the external surface the nerves become more and more delicate, and the meshes of the plexus smaller (fig. 390).

The whole plexus in Mammals occupies essentially the two outer thirds of the thickness of the cornea. A few isolated fibres only supply those parts of the cornea that lie nearer the membrane of Descemet, and these run backwards from the marginal parts of the innermost portion of the anterior plexus formed by the largest nerve fibres. Kölliker states that in Rabbits he has observed the fine lines emanating from these fibres running in a horizontal direction along the membrane of Descemet, and at a short distance from it.

Several subdivisions may be distinguished in the plexus occupying the anterior parts of the cornea. For whilst the thicker nerves proceeding from the posterior parts of the cornea gently bend forward, they expand, together with finer branches, which for the most part run parallel to the surface at a short distance from the line of demarcation between the corneal tissue and the external epithelium (internal to the anterior limiting layer), to form a superficial plexus, enclosing uniform meshes. Emanating from this plexus, delicate vertical or slightly inclined branches (rami perforantes) run to the anterior surface of the cornea and to the anterior epithelium, immediately subjacent to which they break up, either in the form of a brush, as in the Guinea-pig (Cohnheim), or in a stellate manner in a series of finer branches, which again form an exceedingly delicate superficially expanded web, termed the subepithelial plexus (391). From this again fine nerves run forwards at tolerably regular distances from each other between the inferior vertically elongated cells and the more superficially situated spheroidal cells of the epithelium. In this course they run at right angles to the surface. On arriving at the innermost layers of the superficial flattened cells, they give off on all sides their finest terminal fibres, which, after they have previously once or twice or repeatedly divided, often terminate with somewhat swollen extremities in the most superficial epithelial layers.

Seen from the surface, the terminations of the fibres ascending through the epithelium correspond to the nodal points in

which the terminal twigs converging from various directions unite. I have never been able to convince myself of the existence of anastomoses of the various terminal twigs corresponding to such nodal points. Stricker recently showed me a fine plexus in the cornea of the Rabbit, first demonstrated by S. H. Chapman, who had satisfied himself that it was situated on the surface of the external epithelium.

The preceding statements rest chiefly upon observations made on the corneæ of the Pig and Ox, treated with chloride of

Fig. 391.

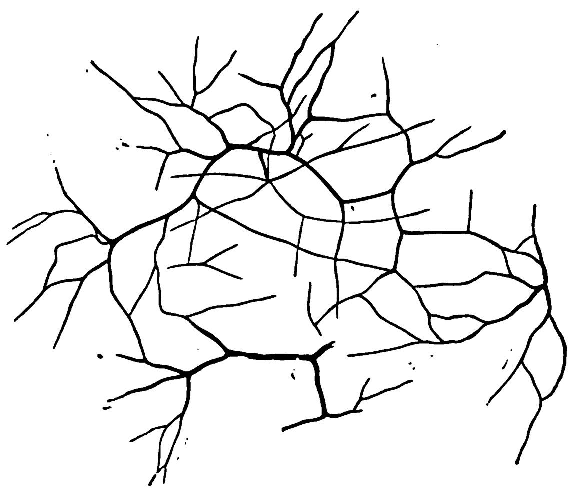

Fig. 391. Portion of the subepithelial nerve plexus of the cornea of the Pig, brought into view by means of chloride of gold.

gold. Similar appearances are, however, obtained, differing only in some points of detail, in the other Mammals that have been examined.

The cornea of the Frog may also be employed in order to obtain extremely good gold preparations (fig. 392), and this possesses the further advantage, that after removal of the epithelium it may be brought under the microscope as a whole, whilst the thick corneæ of the above-named animals, after impregnation with gold and the subsequent reduction of the metal, require to be cut into meridianal and surface slices.

Kühne,* and still more completely, Engelmann,† have followed the distribution of the nerves in the cornea of the Frog examined in perfectly fresh aqueous humour.

Trunklets composed of from five to fifteen or more medullated fibres enter the cornea at six or eight points of its periphery. At several points also isolated medullated fibres, or two together, penetrate its substance. The greater number of these fibres run at first in a straight direction, and for a distance of from 0·2 to 0·5 of a millimeter towards the centre of the cornea; a few only are given off at right angles from the trunklets at the margin of the cornea, and these, after running for some distance parallel to the border, finally turn inwards.

Fig. 392.

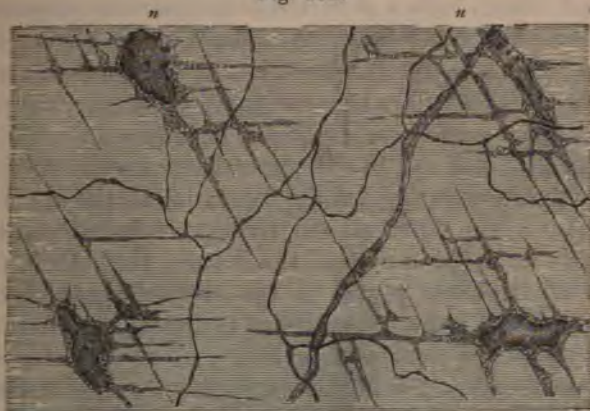

Fig. 392. Portion of cornea of a Frog, prepared with chloride of gold. *n n*, Nerves.

The nerves usually lose their medulla at a short distance from the corneal margin (0·3 to 0·5 of a millimeter); and then, undergoing repeated dichotomous division, form a wide-meshed plexus situated nearer to the posterior than to the anterior surface of the cornea. The occurrence of true anastomoses has not been demonstrated in this plexus of the Frog, any more than in that of Mammals. The presence of sheaths is indicated

* *Untersuchungen über das Protoplasm*, etc., p. 132.

† *Loc. cit.*, p. 15.

both in the medullated as well as in the non-medullated fibres, by nuclei elongated in the direction of the axis of the nerve. As the nerves undergo progressive division, the nuclei become less and less numerous, till they are at length only found in the nodal points of the plexus, which they appear to distend. Ganglion-like structures are thus formed similar to those that have been observed in the corneal nerves of Mammals. Neither in the Frog nor in the Mammal, however, have we to deal with true ganglia in the nodal points of the nervous tissue.

From this plexus, which in the Frog lies almost entirely in one and the same plane, very fine branches are given off at various points, which, both in front and behind the coarse plexus (as far as to about the junction of the anterior with the two posterior thirds), form a close trellis-like nervous expansion in the substance of the cornea. It is doubtful whether any anastomoses exist in this trellis-work, but in the nodal points of its finest fasciculi nuclei are here and there scattered. Here again, however, there are no true ganglionic enlargements. The finest fibres are gradually lost in the corneal tissue, without its being possible to arrive at any definite conclusion of the exact mode. Engelmann* has differentiated the above-described nervous expansion from the nerves of the corneal epithelium, on the ground of its being placed in the proper substance of the cornea.† These last are branches of the above-described coarse plexus, which run vertically or nearly so to the external epithelium. Associated with these are a few fine non-medullated fibres, which pass directly forwards to the epithelium from the periphery. There are collectively from forty to sixty of these nerve trunks in each cornea. At the line of demarcation between the corneal tissue and the external epithelium these nerves give off a variable number of branches, which run in all directions parallel to the surface, and ultimately, to some extent undivided, but in part also after frequent subdivision, reach the long cells of the deepest layer of the epithelium. A close plexus is thus again formed at this point, the terminal fibres proceeding from which reach those cell layers of the epithelium that

* *Loc. cit.*, p. 17.
† *Loc. cit.*, p. 19.

lie immediately beneath the superficial tesselated cells. Specimens prepared with chloride of gold corroborate all that has just been placed before the reader in the most satisfactory manner. I have not observed the passage of the terminal fibres through the superficial layers of the epithelium. The connection stated by Kühne to exist between the above-described corneal nerves and the corneal corpuscles does not, according to Engelmann, occur.

I have sought in vain in a great number of extremely successful specimens of the cornea of the Frog, prepared with chloride of gold, for the fine straight striæ stated by Lipmann* to occur between the finest nerve fibres of the cornea and the nucleoli of the corneal corpuscles in such gold preparations, as well as for the straight striæ which are seen proceeding from the nucleoli of the endothelial cells of the membrane of Descemet. I must rather maintain, from the examination of these gold specimens, that the finest nerve fibres are always to be seen in the corneal tissue running past the corneal corpuscles and their processes, and that therefore no connection of the corneal corpuscles with nerves can be demonstrated.

The Margin of the Cornea.

(*Hornhautfalz, Limbus Corneæ.*)

This is a part to which special interest attaches on account of the transitions and connections that here occur between the above-described layers of the cornea and other tissues.

The external epithelium (*a a,'* fig. 393) is thus continued without interruption into the epithelium of the conjunctiva (*a' a'* fig. 393). We frequently find the external epithelium, together with the anterior limiting layer of the corneal epithelium (lamina elastica anterior), very incorrectly designated the conjunctiva corneæ (as by Kölliker).† The anterior limiting layer in reality does not agree in structure with the peculiar stroma of the conjunctiva bulbi, nor are there any transitional or connect-

* Virchow's *Archiv*, Band xxxviii., p. 218, Taf. vii., figs. 1—6.
† *Handbuch*, p. 647. Leipzig, 1867.

ing fibres between the two. The stroma of the conjunctiva (*kk*, fig. 393) terminates as a thin wedge between the epithelium and the tissue of the cornea. The latter (*b b′*, fig. 393) is continuous with the sclerotic (*b′ b″*), the outer portions of the sclera inclining more towards the central part of the thickness of the cornea than the internal and middle, so that in a meridianal section the part where the transparent cornea and the opaque sclera meet is arcuate (fig. 393). It is very difficult to

Fig. 393.

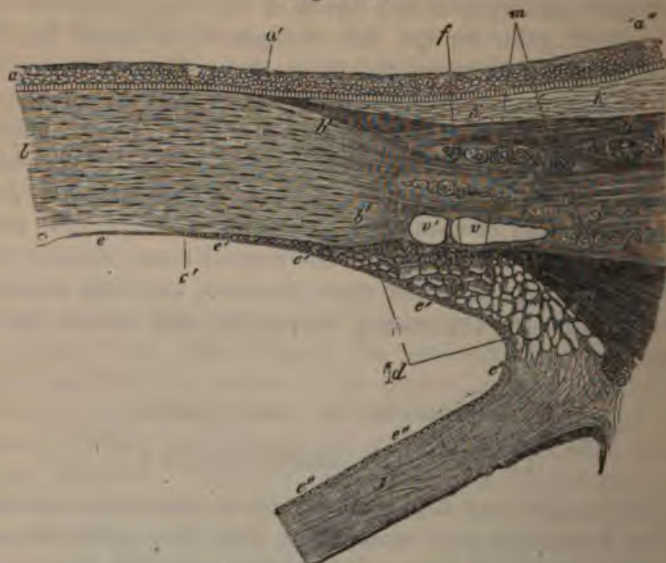

Fig. 393. Margin of the cornea of Man, seen in meridianal section. *a a′*, External epithelium of the cornea; *a′ a″*, epithelium of the conjunctiva bulbi; *b b′ b′*, tissue of the cornea; *b′ b′ b″ b″*, sclerotic; *k k*, conjunctiva; *v v′* canal of Schlemm; *c c′*, membrane of Descemet; *d*, process of the iris; *J*, iris; *e*, endothelium of the membrane of Descemet; *e′ e′ e′*, endothelium of the ligamentum pectinatum iridis; *e″ e″ e″*, endothelium of the iris; *f*, trabecular tissue of the canal of Fontana; *m*, musculus ciliaris.

understand clearly the relation of the corneal tissue with the connective tissue of the sclerotic.

In section and in specimens that have been teased out, the two kinds of fibres appear to pass into one another without

interruption. But on account of the extreme tenuity of the fibrils, both of the cornea and of the sclerotic, this appearance is not to be altogether trusted. Even if they were not continuous with each other, it would be very difficult to separate the two sets of fibres from each other, and to be quite sure of their real mode of termination.

I think it probable that the tissues are only intimately intercalated with each other; for if, by means of simple puncture injection, we break down the corneal tissue in the mode above described, as far as to the periphery, and again extract the injected fluid, we see the corneal tissue presenting a spongy appearance, and running out in the form of thin laminæ intercalated with thin layers of dense sclerotic tissue.

The difference in their chemical characters is a feature that in particular renders it improbable that there is a direct continuity between the fibres of the cornea and those of the connective tissue. Sections of portions of the membranous capsule of the eye, containing the limbus corneæ, that have been boiled in acetic acid and dried, are well adapted for staining both with carmine and picric acid;* and from an examination of such specimens it may be demonstrated that the cornea becomes stained of a yellow colour, whilst the sclerotic, like all connective tissue, stains red. In the cornea the corpuscles alone appear of a red colour.

The membrane of Descemet ($c\,c'$, fig. 393) becomes attenuated at the margin (c'), and indeed in Man is so at a considerable distance from the angle of the anterior chamber of the eye. It does not, however, cease abruptly at the margin, but is connected with peculiar fibres,† which are at first irregular, and interlace at their borders,‡ after which they project with broader or more slender processes, and ultimately form an annulus at the border of the membrane of Descemet,§ on the outer surface of which the gradually attenuating termination of the membrane still continues to lie. With this marginal

* Schwarz, *Sitzungsberichte der Wiener Akademie*, Band lv., Abth. p. 676.

† Henle, *loc. cit.*, pp. 607 and 626.

‡ Schwalbe, *Archiv für Mikroskopische Anatomie*, Band vi., p. 27

§ Iwanoff and Rollett, *Archiv für Ophthalmologie*, Band xv., p.

ring* of the membrane of Descemet the process of the iris is directly continuous (fig. 393, *d*),† as are also the most anterior trabeculæ of the plexus filling the canal of Fontana (fig. 393, *f*); in short, the so-called ligamentum pectinatum iridis of Hueck. The mode of transition in the Ox and Pig is the same as in Man. In the Dog, on the other hand, there is no marginal ring of the membrane of Descemet, and the process of the iris is developed directly from the fibrous cones, forming with their bases a wavy outline to the membrane of Descemet.‡

The endothelium of the membrane of Descemet is uninterruptedly continuous with the endothelium of the process of the iris, and also with that of the most anterior trabeculæ of the canal of Fontana (*e′ e′*), and through this, lastly, with that of the anterior surface of the iris (*e″ e″*, fig. 393).§

* Schwalbe, *loc. cit.*

† Iwanoff and Rollett, *loc. cit.* pp. 19, 36, and 44. Schwalbe, *loc. cit.*, pp. 276—280.

‡ Schwalbe, *loc. cit.*, p. 279.

§ Iwanoff and Rollett, *loc. cit*, pp. 39—43, and 49. Schwalbe, *loc. cit.*, p. 283.

VIII.

CONJUNCTIVA AND SCLEROTIC.

NOTE BY PROFESSOR STRICKER.—A manuscript of Stieda on this subject is in my possession. It was forwarded to me about two years ago, at a time, therefore, at which the author was unacquainted with the plan on which this special chapter would be treated. I have lately felt that the essay in question was too brief for my purposes. In order, therefore, to avoid postponing any longer the appearance of the last part of this work, I have personally undertaken its expansion to many times its original limits. It is consequently, to a great extent, only a compilation. The illustrations have been taken from specimens prepared by E. Klein, and in addition I have made use, besides Stieda's manuscript, and a paper written by E. Klein, of the manuals of Henle, Kölliker, and Leydig, the monograph by E. Brücke, and the treatises of Schmidt and Helfreich. From the last-named four authors I have made literal quotations, indicated by inverted commas. In regard to the nerves alone, have I, aided by a pupil, introduced any original researches, which, however, as the reader will discover, lead to no positive conclusions.

Two portions of the conjunctiva may be distinguished in both the upper and lower lid. One, situated nearer the margin of the lid, is supported and strengthened by a firm ligamentous lamina termed the tarsus, whilst the other, situated nearer to the osseous margin of the orbit, possesses no such support. Henle designates the one the "tarsal portion," and the other the "orbital portion."

Each of the lids is composed of an external layer of skin, of an internal layer of mucous membrane, and of a median layer, which contains the muscular fibres of the orbiculus palpebrarum and of the tarsus.

The *skin* on the outer surface is a continuation of that of the face, and passes directly into the mucous membrane at the free border of the lid. This last covers the inner surface of the lid as far as to the osseous margin of the orbit, where it is reflected upon the eyeball, on which its anterior segment may be traced as far as to the margin of the cornea.

That portion of the membrane which lines the lids is termed the conjunctiva palpebrarum; the point of reflection is named the fornix conjunctivæ; and lastly, the portion covering the eye is called the conjunctiva bulbi. At the inner angle of the eye the conjunctiva bulbi forms a fold, the plica semilunaris, which is considered to be the rudiment of a third lid, or membrana nictitans. Heinrich Müller found smooth muscular fibres in this fold, and these may also consequently be regarded as a rudiment of the muscle of the membrana nictitans.

In the domestic animals Leydig,* and in the elephant Harrison, has observed the presence of dense plates composed of true cartilage.

In the Batrachia the membrana nictitans is specially characterised by its structure and its optical relations. When fresh (living), it is so transparent that after excision, on placing it in the aqueous humour or in the serum of blood, it may be examined with the highest powers; and if the somewhat thicker margins are cut away, a perfectly plane expansion is obtained, admirably adapted for examination with high powers.

In such specimens the opportunity is afforded of investigating, whilst perfectly fresh, epithelium, connective tissue, bloodvessels, nerves, and glands. Above all, the bloodvessels are here brought into view more beautifully than is the case with any other known organ of the adult animal after removal from the living body. The opportunity is also afforded of examining the simple flask-like glands, and at all depths their excretory ducts as they perforate the external epithelium. Lastly, medullated nerve fibres may be examined, either singly or united into fasciculi, in regard to which it may be said that they at least approximate very closely to their living condition.

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* *Lehrbuch der Histologie*, 1857.

Several years ago Stricker observed spontaneous contractions in the capillary bloodvessels of such nictitating membranes. The statement, however, has not been corroborated by any other observer.

The integument both of the upper and of the lower lid is thinner than that of the face, and easily moveable on the subjacent tissue. The epidermis is composed of a thin corneal layer and a rete Malpighii, formed of several layers of polyhedric

Fig. 394.

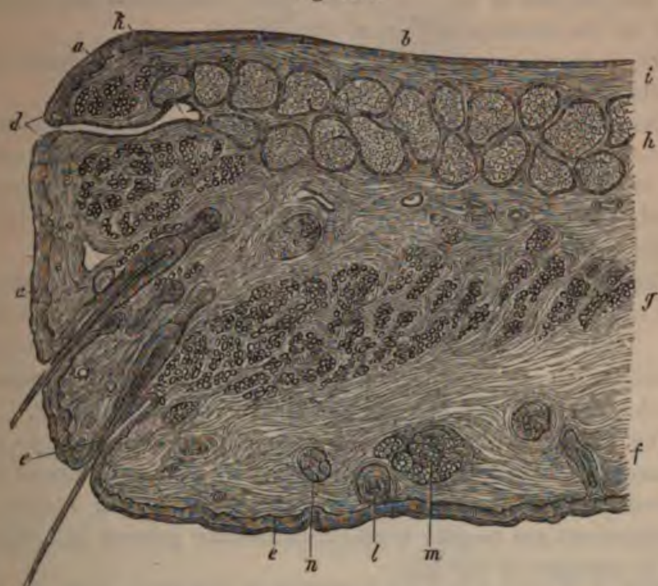

Fig. 394. Vertical section through the lid of a new-born child, as seen with a Hartnack's microscope, ocul. 3, obj. 2. *a*, Epithelium of the free margin of the lids; *b*, epithelium of the conjunctiva palpebrarum; *c*, epidermis of the skin of the lid; *d*, portio Riolani; *e*, cilium; *f*, cutis; *g*, musculus sphincter orbiculus; *h*, Meibomian glands; *i*, connective tissue between the Meibomian glands and the epithelium; *k*, excretory ducts of the Meibomian glands; *l*, hairs; *m*, sebaceous glands; *n*, sudoriparous glands.

cells. The corium in the new-born child presents only a few small and irregular papillæ, but in the adult the papillæ are well developed, and contain vascular loops. It is composed of

loose fibrillar connective tissue, in the anterior layers of which especially are many branched cells, and it is moreover poor in elastic fibres.

The subcutaneous tissue consists of a superficial dense, and of a deeper and less dense, fibrous structure. A few fat cells appear in the deeper layers, near the margin of the orbit. The anterior layer of the integument extends over about one half of the margin of the lid, which is about two millimeters in thickness; the rete Malpighii, however, is here much thicker, and the papillæ of the corium are more numerous and larger than on the anterior surface of the lid.

The integuments of the lids are provided with hairs and glands.

The *hairs* of the anterior surface are larger in the new-born child than in the adult, in whom they are sparingly distributed and very thin and small. The hair follicles and the sebaceous glands belonging to them dip into the superficial denser layer of the subcutaneous tissue.

The cilia are slightly curved, and are planted in from two to four rows into the anterior integument at the margin of the lid. Their circular muscular layer is very strongly developed, especially in the deeper part of the follicle. A sebaceous follicle opens on each side of the neck of the hair follicle.

The duration of the life of each cilium, according to the researches of Moll, is about 100 days. As a consequence of the obviously rapid succession of hairs, the several stages of development are usually found coincidently present in sections of the margins of the lids.

Besides the succession of the hairs, which proceeds in the manner already described in vol. ii., p. 255, a formation of new hairs occurs, independently of the already existing hair follicles, by direct involution of the rete Malpighii.

The *sweat glands* in the anterior integument are small roundish bodies, composed of a canal convoluted into a knot. A short excretory duct springs from the knot, and runs in a tolerably straight direction towards the surface, where, after perforating the thin epidermal layer, it opens. As the epidermis is very thin, the corkscrew-like portion of the course of the duct is here scarcely perceptible.

In the lower segment of the anterior layer the sweat glands are of quite different form. Each gland appears as a cylindrical canal, which, commencing by a cœcal extremity, runs with a slightly sinuous course. Whilst the other glands are arranged vertically to the surface, and therefore, on account of the thinness of the anterior integuments, can only be extremely small, the glands of the lower segment just alluded to are

Fig. 395.

Fig. 395. Longitudinal section through the root of a cilium, from a new-born child, seen with a Hartnack's microscope, ocular 3, objective 7. *a*, Papilla of the hair; *b*, longitudinal fibrous membrane of the hair follicle; *c*, transversely striated muscle; *d*, vitreous membrane of the hair follicle; *e*, cells of the external root-sheath; *f*, layer of cells covering the vitreous membrane of the papilla; *g*, circular muscular layer of the hair follicle.

considerably larger. They run parallel to the surface; their blind extremity is situated much higher, between the anterior and middle lamellæ, whilst the excretory duct of the gland opens below, near the margin of the lid. The duct is circular on section, and possesses a connective-tissue sheath sometimes

containing longitudinal bands of smooth muscular fibres. Internally it is lined by a layer of cells which are a continuation of the rete Malpighii; somewhat deeper they are replaced by columnar cells, which in the new-born child extend to the fundus, but in the adult are exchanged, in the deepest portion of the tube lying in the looser layer of the subcutaneous connective tissue, for cubic cells. They sometimes contain a yellowish-brown pigment. Near the external orifice the canal becomes contracted, and usually opens like a funnel into the follicle of a cilium, though sometimes separately. The cells lining the tube pass gradually into those of the epidermis. This peculiar variety of the sudoriparous glands was first described by Moll.*

The connective-tissue fasciculi of the deeper loose layer of the subcutaneous tissue form, by decussation with the connective-tissue trabeculæ of the corresponding layer of the submucous tissue, a plexiform tissue, situated about the middle of the thickness of the lids, in the meshes of which the fasciculi of the musculus sphincter orbicularis, which run parallel to the margin of the lid, are imbedded. These are arranged one above the other, and extend from the orbital margin towards the free border of the lid in such fashion that the uppermost fasciculi of the lower eyelid and the lowermost of the upper eyelid are situated between the root of the most anterior cilia and the skin covering the anterior surface of the lid.

A few fibres are given off from the innermost fasciculi, which partly penetrate between the cilia, and partly run towards the anterior border of the lid.

Besides this muscle, the lid contains also the transversely striated ciliaris Riolani. This almost always consists of two portions, which both run parallel, and close to the margin of the lid.

The larger portion of this—really a large fasciculus—lies between the hindermost cilia and the excretory ducts of the Meibomian glands, whilst the smaller portion, consisting of from three to five small fasciculi, is imbedded close to the posterior border of the lid, between the mucosa of the conjunctiva and the neck of the excretory duct of the Meibomian glands.

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* *Bydragen tot de nat. der oagleden.* Utrecht, 1857.

The plexiform tissue which traverses the fasciculi of these two portions, and in the interstices of which each transversely striated muscular fibre is imbedded, is in the new-born child composed of a very delicate plexus of branched nucleated cells.

The *Meibomian glands* number from thirty to forty in the upper and from twenty to thirty in the lower lid. They are imbedded in a dense tissue situated between the middle and posterior layers, which by manipulation can be separated from the other tissues, and which has received the name of the cartilage of the eyelid or tarsus. In sections it appears that the so-called tarsus is continuous with the connective-tissue substratum of the middle and posterior layers, and is differentiated only by the peculiar arrangement and appearance of its tissue from that which is around it.

The tissue of the *tarsus* is composed of more or less regularly arranged fasciculi of connective tissue, the fibres of which are broader, more lustrous, and resistant to the action of reagents than those of fibrillar connective tissue. In the immediate vicinity of the glands the fasciculi run horizontally from before backwards, forming larger or smaller arches around the several acini. Here and there the several fibres run obliquely, and decussate with each other. Near the muscular layer on the one hand, and the connective tissue on the other, the fasciculi pursue an opposite direction. They here run parallel to the surface of the lids, and throughout their whole extent from above downwards. Between the fibres, or attached to certain fibres, are distributed, though not always in large numbers, elongated nuclei, with pointed extremities. No cartilage cells have hitherto been found in them. The transition of the tarsal connective tissue into the connective tissue of the adjoining layer occurs gradually, whilst ordinary fibrillar connective tissue takes the place of the stiff fibres of the tarsus.

The Meibomian glands are arranged in linear series parallel to the surface, and their excretory ducts open on the free border of the lid, near its posterior margin; their blind extremities do not quite extend to the line of junction of the conjunctiva palpebræ and fornix conjunctiva. Each Meibomian gland is composed of a relatively wide excretory duct, from all sides of which short bulbous acini are given off. The excretory

duct is narrowest close to the funnel-shaped opening, where it forms the neck of the excretory duct; towards the fundus it is beset with manifold dilatations termed the acini. Each acinus is a spherical or ovate body, that appears filled with cells up to its opening into the excretory duct. There are many points in each gland where several closely approximated acini do not open into the principal excretory duct, but unite to form a secondary duct, which then opens into the main

Fig. 396.

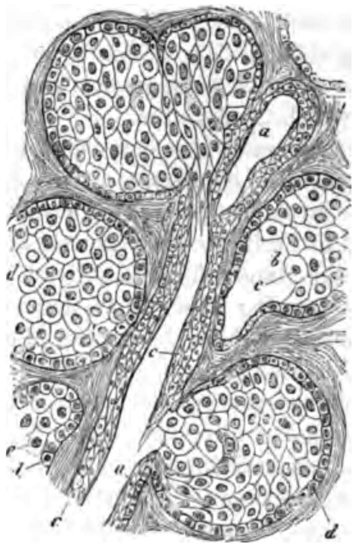

Fig. 396. Longitudinal section through a portion of a Meibomian gland, from a new-born child, examined with a Hartnack, ocul. 3, obj. 8. *a*, Excretory duct; *b*, acini; *c*, laminated epithelium of the excretory duct; *d*, layer of cubical epithelial cells investing the membrana propria; *e*, epithelial cells of the acini containing fat.

duct. In this case the latter appears considerably dilated at such points.

The epithelium of the principal excretory duct is laminated and tesselated. The two or three superficial rows are flattened, and contain oblong nuclei. They are succeeded by one or two tiers of polyhedric cells with spheroidal nuclei, which are again followed by a row of obliquely placed granular

(when fresh) cellular bodies of columnar or cubical form, which become deeply stained with carmine and chloride of gold, and which are in immediate contact with the membrana propria.

The lowermost tier of cells, composed of cubic or columnar cells, and the uppermost tier, composed of flattened cells, are prolonged into the secondary excretory ducts of the several acini. In each acinus the presence of a membrana propria may be distinguished, which sometimes appears to be structureless, and sometimes (in specimens prepared with chloride of gold) to be provided with a network of flat branched structures. The membrana propria is lined by a layer of granulated cubical or short columnar cells, which stain easily and deeply, and contain spheroidal nuclei in their interior. This layer of cells is a direct continuation of the deepest cell layer of the excretory duct. The interior of the acinus is filled with sharply defined bodies flattened by mutual pressure, which increase in size towards the interior of the acinus, and when fresh appear to be uniformly filled with a highly refractile substance (fat). If these bodies are examined in specimens which have previously been immersed in alcohol and oil of cloves, and then mounted in dammar resin, each of them presents a sharply defined nucleus, and in some cases also an extremely fine network in their interior.

Near the fornix conjunctivæ, and in the portion of the submucous tissue termed the tarsus, lie certain *gland tubes* which probably secrete *mucus*, and are extraordinarily convoluted.

The gland tube is bounded by a membrana propria, on which in general there is only a single layer of columnar granular cells, though occasionally there appear to be two rows of tesselated cells. The short excretory duct of the gland, which exhibits the same structure, perforates the mucous membrane of the conjunctiva obliquely, in order to open into the sac of the conjunctiva.

These glands probably correspond to the acinous mucous glands described by Krause and Sappey as situated at the line of transition of the conjunctiva palpebrarum into the fornix.

The posterior layer of the lid, the conjunctiva, when fresh, is of a delicate pink colour, and presents a velvety surface. It is not everywhere of equal thickness, but increases in this

respect from the margin of the lid backwards, becoming attenuated again where it is reflected upon the globe of the eye. The palpebral conjunctiva is not smooth, but furrowed, and traversed in all directions by groove-like depressions. These, which are sometimes deep, sometimes shallow, sometimes straight, sometimes oblique, decussate with one another, and thus form a number of irregularly shaped islands, which have been described by authors as papillæ or papilliform elevations. In some instances the grooves do not form a plexus intercom-

Fig. 397.

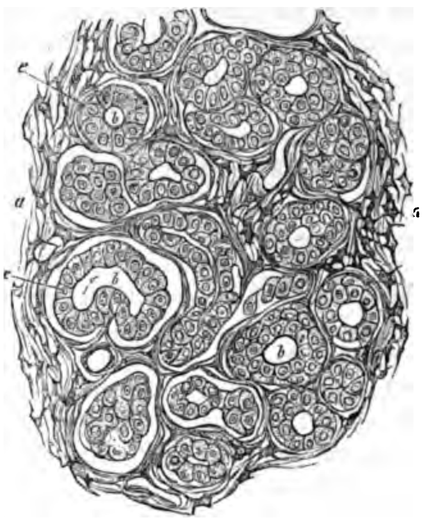

Fig. 397. Transverse section through that portion of the tarsus in which the tubular glands lie,. examined with a Hartnack's instrument, ocular 3, objective 8; specimen prepared with chloride of gold. *a*, Cell plexuses of the tarsus; *b*, tubular glands; *c*, epithelium of the gland tubes.

municating at all points, but appear completely isolated from one another in the form of fissures or furrows, like depressions near the margin of the lid; the furrows are numerous, but shallow; at some distance from the border they are deeper, and at the line of reflection they are continued, without any sharply defined line of demarcation, into the depressions here

found between the longitudinal folds that give its plicated aspect to this segment of the conjunctiva.

True papillæ, however, do occur. In the new-born child vascular papillæ are only met with near the fornix conjunctivæ. But it is otherwise in adults; in them small and isolated papillæ are met with near the border of the lid, which increase towards the fornix, both in height and in breadth. Where there are no papillæ on the conjunctiva, dense plexuses of extraordinarily wide bloodvessels are distributed immediately beneath the epithelium; but where the papillæ occur, a loop ascends from the superficial plexus into each papilla.

The epithelium of the conjunctiva is laminated; it is thickest over the posterior half of the free border of the lid; from the posterior border of the margin of the lid it rapidly diminishes in thickness, and on the posterior surface of the lid is composed of a superficial layer of greatly flattened cells, each containing an oblong compressed nucleus, succeeded by two or three layers of polyhedric cells, and finally by a deep layer of columnar cells.

The thin and delicate conjunctival mucous membrane of the lids is composed of a loose connective-tissue matrix, in which elastic fibres are only sparingly present.

On the other hand, the mucous membrane is extraordinarily rich in branched cells, which, especially just beneath the epithelium, form a beautiful plexus.

I extract from the recently published treatise of Schmid, "On the Lymph Follicles of the Connective Tissue of the Eye," the following statements on the structures described in that work.* Bruch first mentioned in an appendix to his account of Peyer's patches in the small intestine, the existence of similar structures in the conjunctiva of the lower lid of oxen. He described them as closed sacs, visible to the naked eye, in the pulp of which a vascular plexus of capillaries is distributed. These sacs are termed Bruch's clusters (Haufen). Stromeyer stated that follicles were present both in domestic and wild animals, and that they are chiefly situated near the inner canthus of the eye,

* *Brunmüller*. Wien, 1870. The literature of the subject is fully given in this work.

and beneath the membrana nictitans, and are pre-eminently developed in the upper lid. He regarded them as pathological structures on account of their irregularity and inconstancy, on account of the roughness that results from their presence, and on account of the morbid phenomena they occasion, as, for example, the injection which extends to the vessels of the bulb itself. Henle designates them "trachoma glands." W. Krause also found lymph follicles in the Rabbit and Fox, and in Birds. He first maintained that their presence was general, and considered them to be physiological structures.

Kleinschmidt found the same kind of follicles in Man and in domestic animals.

Huguenin (under Frey's direction) gave a similar description. He found the vessels of the connective tissue narrower, and the trabeculæ thinner, near the periphery of the follicles, whilst at the centre the meshes are larger, and the trabeculæ thinner. The tissues lying between the follicles are traversed by lymph cells. In this tissue lymph paths occur in the form of elongated oval spaces without trace of vascular walls. Blood vascular injections exhibited a rich system of branches in the interfollicular substance. The follicles are surrounded by arterial vessels, but their caps are poorly supplied.

Blumberg (under Stieda's direction) stated that in the Pig the mucous membrane of the conjunctiva, with the exception of the tarsal portion, is composed of adenoid tissue, and possesses trachoma follicles; these last however are absent in young Pigs. In the Dog the matrix of the mucous membrane, as well as that of the conjunctival cœcal sac, is composed of adenoid tissue; in the tarsal conjunctiva, the reticular tissue contains only a sparing amount of lymph cells. Numerous trachoma follicles are present in the mucous membrane of the membrana nictitans, and often also upon its external surface; on the tarsus, on the other hand, it is only occasionally that trachoma follicles are met with in great numbers; at the line of reflection, trachoma follicles pass apparently by a process of gradual transition into the adenoid tissue; in the conjunctiva bulbi, trachoma follicles frequently occur. In new-born Dogs neither adenoid tissue nor trachoma follicles are present. Similar relations exist in the Rabbit, Horse, and Ox; in the Cat,

on the other hand, the matrix consists of fibrillar connective tissue, and there are no trachoma follicles. Lastly, Wolfring also, like Stromeyer and Blumberg, regarded the lymph follicles of the connective tissue as pathological structures.

Schmid's investigations have been made on Dogs, Pigs, Sheep, and children at various ages, beginning from the first week of life, and in adult Rats, Cats, and Otters. He found that the follicles in the above-named animals are usually present at the inner angle of the eye, and at the line of reflection of the conjunctiva of the third lid upon the bulbus. In order to make the follicles distinctly recognisable with the naked eye, he exposed the organ for a few hours to the action of a half per cent. solution of hydrochloric acid.

He was unable to discover any follicles in animals during the first week of life. The tissue of the conjunctiva palpebrarum and fold of reflection is then a diffused adenoid tissue; only a relatively very small part of the conjunctiva bulbi near the line of reflection presents this form of tissue.

During the second week of life we find here and there a greater abundance of vessels and a larger accumulation of cells. The connective-tissue trabeculæ and large bloodvessels present a peculiar disposition and arrangement around these spots, the outline of which is rendered still more prominent in consequence of the inflection either of the epithelial surface or of the submucous tissue. The follicle is complete at the end of the third week of life.

The structural relations described by Schmid show that we are now dealing with bodies that are precisely similar to the lymph follicles.

It only remains to mention what has been done in regard to the lymph paths. Schmid has effected their distension by means of simple injection with a hand instrument. He recommends the immediate neighbourhood of the limbus as the most appropriate for this purpose. He found, as Teichmann had already shown to be the case in regard to the limbus conjunctivæ, that a superficial and a deep plexus of lymphatics, connected by many anastomoses with one another, are distributed throughout the entire cornea. The lymphatics of the limbus conjunctiva are connected with those of the rest of the

conjunctiva by sparing anastomoses only. The superficial plexus is characterised by small and delicate canals which have a very uniform outline. Short lateral, cœcal, and more or less pointed or broad, processes are given off from them. The deeper-lying canals, on the other hand, are broader, with more irregular contours, and often present the characteristic constrictions corresponding to valves. Speaking generally, it may be said that the limbus conjunctivæ possesses a very fine-meshed plexus, whilst the anastomoses, especially of the superficial layers, of the bulb are wider, and, on the other hand, those of the fold of reflection, as well as of the lids, are closer and more numerous.

The conjunctiva is reflected from the lid upon the anterior surface of the bulb in the form of a thin membrane attached to the adjoining parts by very loose tissue, and thus forms the segment known as the *fornix conjunctivæ.* The epithelium that covers this portion of the conjunctival sac differs in many particulars from the epithelium of the connective tissue of the lid. It consists of from two to four layers; the most superficial are conical, or rather columnar, whilst the succeeding layers are composed of polyhedric or small spheroidal cells. There are no well-marked papillæ on this part of the membrane, which differs but little from that of the lid. It contains numerous elastic fibres, as well as branched cells and superficial plexuses of wide capillaries.

In regard to the *conjunctiva bulbi,* it only remains to be stated that it is covered by a laminated pavement epithelium, with the same number and kind of layers as the epithelium of the free border of the lid; the surface of the mucous membrane is not smooth, but exhibits scattered well-developed papillæ, which diminish in size and number towards the cornea, and in the immediate neighbourhood of that membrane altogether disappear. The epithelium also diminishes in thickness towards the margin of the cornea, where it becomes thinnest, but from thence onwards again becomes thicker.

The epithelium of the cornea is a direct continuation of the epithelium of the conjunctiva bulbi, though the following points may be regarded as the chief differences between them. The epithelial cells of the deepest and of the middle layers of

the former are more sharply defined than those of the conjunctiva bulbi, and at the same time more transparent. In many animals the epithelial cells of the above-named layers of the conjunctiva bulbi close to the corneal border contain dark pigment granules in the nucleus and in the substance of the cell.

Helfreich * has written a treatise on the *nerves of the conjunctiva,* and the following excerpt will show the state of our knowledge respecting them :—

Fig. 398.

a

b

c

d

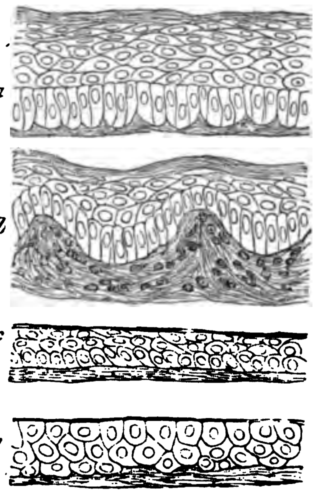

Fig. 398. *a*, Epithelium of the conjunctiva of the border of the lid ; *b*, epithelium of the conjunctiva bulbi ; *c*, epithelium of the conjunctiva palpebrarum ; *d*, epithelium of the fornix conjunctivæ. All taken from sections of specimens prepared with chloride of gold, and drawn as seen with a Hartnack's instrument, ocular 3, obj. 8.

" We are indebted to W. Krause† for the first observation in regard to the ultimate distribution of the nerves of the conjunctiva. According to his description, the nerves distributed to the conjunctiva, after repeatedly forming plexuses and exchanging fibres, penetrate by degrees into the upper layers of the propria, and end in peculiar terminal organs, which he

* Würzburg, 1869.

† *Ueber terminale Korperchen,* 1860.

names 'terminal bulbs,' and in which he recognizes a connective-tissue sheath, with nuclei, an internal bulb of finely granular, dull-shining material, and in the interior of this a pale terminal fibre, with a somewhat bulbous thickened end. Krause was successful in discovering these terminal bodies in Man, but in only a few animals, as in the Horse, Ox, Sheep, and Pig. In these animals their number was also proportionately small, and their distribution highly dissimilar and irregular. He observes that in some instances not one of these terminal apparatuses can be discovered over a considerable extent of surface, whilst in others they may be found accumulated in large numbers, closely aggregated upon a few fibres radiating from a common centre.

On account of their variations, no attempt was made to obtain their precise number, though on a rough estimate he concluded that, in the various animals, as in Man, the number of terminal bulbs present in the connective tissue appeared to be the same, and that consequently there was as remarkably small a total number of nervous terminal apparatus in the conjunctiva as in the skin of the last phalanges of the fingers. The form presented by the terminal bulbs varies in Man, as well as in different animals. In the former, as in the Quadrumana, they are rounded or almost spheroidal; in other animals they have in general a more elongated, oval, or even well-marked cylindrical contour, and they are then either straight or slightly bent. In regard to their dimensions, he states that they usually stand in direct proportion to the size of the animal, and that they also increase to some extent with the growth of the body, since, though they present the same characters in young animals as in old, they are of somewhat smaller size. In regard to their minute anatomy, the sheaths of the terminal bulbs consist of delicate connective tissue, which is continuous with the neurilemma of the entering doubly contoured fibre, and in which are scattered numerous for the most part elongated nuclei. The internal bulb, which is the chief constituent of the whole organ, is finely granular; and the terminal fibre, which is the extremity of the doubly contoured fibril, is imbedded in its substance. At its distal extremity it exhibits a slight bulbous enlargement, and usually ends at some distance from the anterior boundary of the internal bulb. In Man, several terminal fibres are

usually met with in the interior of each bulb, which sometimes form a series of coils, and in most instances originate from a single afferent fibre."

The statement of Krause, resting on these observations, to the effect that the terminal bulbs constitute the only mode of termination of the conjunctival nerves, was energetically disputed by J. Arnold,* who, on the one hand, regarded the terminal bulbs of Krause as not pre-existent, but as artificial products, and ascribed their origin to the method of preparation adopted by Krause, whilst, on the other, he described as the true terminations of the nerves, a pale plexus of nerve fibres situated in the more superficial layers of the tissue. Owing to his mode of preparation, which consists in macerating the specimen in acetic acid, or in rendering it transparent by alkalies, Krause, he concluded, could not observe this plexus, since the first reagent would destroy the most superficial layer of the mucous membrane, whilst the second would render all the parts so transparent that these pale fibres could not be perceived. The terminal bulbs described by Krause might, he thought, arise through the rupture of the doubly contoured fibres, partly effected in the act of preparing the specimen, but partly also occasioned by the reagents applied by Krause, which lead to an escape of myelin, and rolling up of the torn fibres. Both circumstances would occasion the illusory appearance of the internal bulb, the neurilemma of the torn fibres representing the connective-tissue sheath of the terminal bulbs, and the terminal fibre being represented by the axis cylinder. Everywhere the distal prolongation of the fibre may be discovered, and it is also easy to discover ends and fragments of the nerve sheath at the periphery of the so-called terminal bulbs.

The objections raised by Arnold have found opponents in Lüdden and Frey, who again admit the existence of terminal bulbs as a certainly established fact. Helfreich gives the following details from his own researches:—

The nerves destined for the conjunctiva pass to it from the inner and outer canthi, where the several branches are given off from the main trunks, and pursue a more or less sinuous

* Virchow's *Archiv*, Band xxvi.

course. It is, however, chiefly the trunk entering at the inner commissure that contains the principal portion of the fibres, and is hence remarkable for its size and the much larger number of its branches. He was able to establish this type of nerve division in all the specimens prepared from various animals that he examined; the less important differences met with in a few instances, as, for example, a more or less superior point of entrance of the internally situated main trunk, are only incidentally mentioned. In consequence of the speedy division and subdivision of the two principal trunks, and especially of the inner one, a close and delicate plexus is formed, in which an exchange of a few fibres takes place between the smaller branches. The principal portion of the branches constituting this plexus stretches toward the anterior half of the conjunctival sac, and to its palpebral portion, whilst the fornix contains but few small branches, and the visceral lamina of the same receives generally only a third or fourth part of the nerves passing to it. As has been already remarked, the number of the nerves entering at the inner commissure of the conjunctival sac is far greater than at the outer side, and this preponderance continues to be so expressed (notwithstanding the large number of fibres given off for the supply of the membrana nictitans), in the further distribution of the nerves, so that the branches coming from the inner side pass beyond the antero-posterior median line of the conjunctival expansion, and thus only the smaller lateral portion of the sac is supplied with fibres coming from the outer commissure. Moreover, so far as regards another relation, namely, the proportion of nerves distributed to the upper and lower lids, some variations occur, in accordance with the special anatomical relations of the particular animal under examination. In the Frog, for example, where the membrana nictitans, by virtue of its peculiar arrangement and its large extent, not only represents the lower lid, but also fulfils the greater part of the functions which in other animals are performed by the upper lid, the richness of its supply of nerves may considerably exceed that of the latter. A modification again occurs in Birds, where the membrana nictitans is indeed present as an integral constituent of the conjunctival sac, but in which the lower lid surpasses the upper in anatomical extent

and physiological importance. On the other hand, in regard to the higher animals, the Mammals, and Man himself, the opposite relation to that of the Frog holds, and the upper lid is more richly supplied with nerves than the lower.

Finally, in regard to its origin, the internal medial trunk is to be regarded as one of the terminal branches of the infra-trochlearis, and the lateral as the termination of the nervus lachrymalis, both of which proceed from the first branch of the trigeminal nerve.

After forming the coarse-meshed plexus in the subconjunctival, and in the deeper layers of the conjunctival tissue, the nerves, continually becoming smaller till they are composed of only a few fibres, gradually pass forwards. These branches never exhibit any plexiform anastomoses. The relation of the smallest trunks, which are still composed of from two to three doubly contoured fibres, is in some animals, as, for example, in the Frog, so regular that it may here be minutely described. After the trunks of the last order have extended as far as to the plane just beneath the last layers of the vascular capillary plexus, division once more occurs, owing to which the still doubly contoured fibres, as they part from each other, run in a direction nearly at right angles to that of the trunk, and may be followed for considerable distances, maintaining a perfectly straight course, or being but slightly sinuous. A system of more or less parallel doubly contoured fibres is thus produced, which lies beneath the capillary network. In other animals the course and mode of division of the ultimate trunklets composed of doubly contoured fibres is less regular; and it is only necessary to state that, rising above the vessels in the most diverse vertical oblique direction, they gradually reach the surface, where, in the last division of the dark fibres, their transition into non-medullated fibrils takes place. An exception to this is met with in certain fibres which only gradually ascend, as Helfreich satisfied himself, not in surface preparations, but in a considerable number of vertical sections in various animals. In this case a single fibre proceeds from a trunklet that is still composed of a large number of doubly contoured fibrils, and runs nearly in the middle of the matrix of the conjunctiva; the fibre at this point

suddenly loses its medullary sheath, and, ascending vertically again, bends at right angles to its former course to enter the subepithelial plexus of pale fibres, in which it runs for some distance, as may be easily demonstrated in more obliquely made vertical sections.

Reference must not be omitted to those pale fibres which enter the tissue on the same plane as the larger vascular and nervous trunks, and are characterised by a very sinuous course, and by preserving their original direction for a considerable distance. In consequence of this they only gradually pass forwards, and then entering the general subepithelial nervous expansion, can no longer be separately followed. In this course they often come into relation with the larger vascular trunks, immediately around and on which they form numerous plexiform loops, and run, sometimes for long distances, upon the vessels themselves. But as these relations can only be observed in preparations of moderate size, we must often abandon the attempt to follow them out. Nevertheless, Helfreich was successful in a large number of cases in following them upwards towards the epithelium, and saw them enter the general plexus found beneath this. During their long course they exhibit numerous varicosities and many clusters of nuclei.

As already mentioned, the trunklets of the last order are composed of two, or at most three, doubly contoured fibres. The latter lose their medullary sheath at the point of their ultimate division, but not previously, during their common course. A nucleus usually occupies the angle of division, and this shows also a slight varicose enlargement, at which point the pale fibres commence.

These fibres are of extraordinary length, and a single fibril may often be followed through several fields of the microscope; they usually run in a straight direction, and consequently only present slight and occasional loopings, or a gradually bending upwards to a higher level, crossing and interweaving with the capillary plexus. The number of these non-medullated fibrils as they run upward through the capillary plexus is extraordinarily great, so that the total number of the fibres running between the capillaries and immediately subjacent to the epithelium exceeds many times that of the fibres present in the

different trunks. It is self-evident that their number must be very different in the several regions of the conjunctiva, sometimes being relatively small, so that a direct estimate of their number can be effected, and the several elements may be readily followed to their termination.

Thus, as the result of the several larger fibrils running for long distances with continual subdivision, and their lateral branches repeating this process, a very dense plexus of large and also of extremely fine pale fibres is produced, which gradually extends through the layer of blood capillaries to the inferior surface of the epithelium. The fine fibrils found immediately beneath the epithelium have themselves also a very long course, give off innumerable fine branches at acute angles, and ultimately terminate close beneath the plane of the deepest cell layer, where they may easily, in preparations freed from the epithelium to which the account hitherto given applies, be discerned amongst the cells that here and there remain attached.

Morano* has been engaged for several months, under Stricker's direction, in ascertaining the mode of termination of the nerves of the conjunctiva. The positive results obtained, however, are very few in number. They believe, though they are by no means certain, that they were able to follow the nerves in some instances upwards between the epithelial cells. These researches have, however, rendered it probable that more fortunate microscopists may be able to follow the nerves into the epithelial stratum.

TUNICA SCLEROTICA.

The sclerotic† is bounded in front by the cornea, whilst posteriorly it is separated by a constriction from its continuation, the fibrous sheath of the optic nerve. Where the optic nerve enters the cavity of the sclerotic, the connective tissue investing its fasciculi joins the tissue of the sclerotic. This junction remains even after the optic-nerve fibres have been removed by

* *Centralblatt*, April, 1871.

† Brücke, *Anatomische Beschreibung des menschlichen Augapfels*, (Anatomical description of the human eye.) Berlin, 1847.

maceration, in the form of a thin lamina perforated by many small holes, which is continuous with the internal surface of the sclerotic. This lamina is the so-called lamina cribrosa. The foramina correspond to the several fasciculi of the optic-nerve fibres which traverse it. Near its centre are two close together, of large size, through which the retinal vessels pass.

The sclerotic becomes denser and more uniform in structure as we pass from without inwards. Irregularly shaped flat pigment cells, with clavate or radiating processes, are deposited in the very dense tissue lining its smooth inner surface, and this is especially the case in dark eyes, giving to it, when they are present in large numbers, a brownish aspect.

The arrangement of the fibres of the sclerotic was first described by Valentin.* Brücke was only able to support his statements so far as to say that, speaking generally, there were antero-posterior and circular fibres in the sclerotic, forming by their decussation a dense tissue, and that the fibres of the tendons of the recti muscles, after they have reached the sclerotic, spread out in a fan-like manner, and, dipping into the mesh-work of the sclerotic, essentially strengthen its anterior portion.

That the sclerotic fibres are composed of connective tissue has already been shown at p. 79, vol. i. Cellular elements resembling the corpuscles of the cornea are distributed through the matrix. If a point of nitrate of silver be drawn across the sclerotic of a live Rabbit, the delicate lines of the serous canals may be seen in surface sections, when it is completely reduced. On the other hand, preparations made with chloride of gold give a positive to the negative images of the silver method. I have, indeed, only seen the latter in a preparation exhibited to me by Dr. Carmelt, of New York; in this instance, however, they were so sharply defined that no doubt of their presence could exist. The cells that lie in these spaces contain, in many Mammals, pigment granules.†

In Birds the sclerotic is composed of hyaline cartilage, invested both externally and internally by connective tissue.

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* *Repertorium*, Band i., Heft. iv., p. 301.

† Leydig, *loc. cit.*

At the anterior margin of the sclerotic, and sometimes around the entrance of the optic nerve, there is in Birds a bony ring, composed of a series of plates.

Hyaline cartilage is also present in the sclerotic of Amphibia and Fishes. Helfreich* took the opportunity, in his paper on the nerves of the sclerotic, to make a few observations upon the structure of the sclerotic of the Frog, which I shall here reproduce.

The connective-tissue layer closely adhering by its inner surface to a slightly rose-coloured layer of cartilage, with extraordinarily distinct and beautifully marked cells, appeared of a dark olive tint, composed of compact parallel and vertically arranged fibrous bands, to the outer side of which was applied, though separated by a sharp line of demarcation, the investing looser sheath of connective tissue. Antero-posterior sections of the sclerotic carried through its whole extent showed that the connective-tissue and cartilaginous layers vary in thickness at different points. The cartilaginous layer was thickest at the posterior pole of the globe of the eye, and diminished rapidly at the anterior part, terminating by a rounded edge just in front of the plane of insertion of the recti muscles. The connective-tissue layer exhibited the converse relation in regard to its thickness at various points. The cartilaginous layer was completely homogeneous, and never presented any interruptions or openings for the passage of vessels and nerves; whilst in the connective-tissue layer these last presented the same clean aspect and elegance as in surface views. In the posterior parts of longitudinal sections the coarser trunks and doubly contoured fibres were visible, and towards the anterior portions, as far as to the border of the cartilaginous layer, and even beyond this, the fine light-blue violet-tinted axis cylinders were seen running for considerable distances either straight or with a slightly sinuous course. Here and there they exhibit slight varicose enlargements, and in regard to their course it was noticeable that they gradually approximated t[illegible] of demarcation between the connective-tissue and the ca[illegible] layers.

* *Loc. cit.*

The larger nerve trunks, everywhere composed of somewhat separated doubly contoured nerve fibres, exhibited after undergoing manifold division, and after running for a greater or less extent forward, the most distinct connection with the already mentioned longitudinally running axis cylinders, with which they are continuous in such a manner that the ultimate trunklets, composed of two doubly contoured fibres, lose their medulla at the point of division. This suppression of the medullary sheath, as well as the course of the pale fibres towards the line of demarcation of the connective-tissue and cartilaginous layers, could be satisfactorily demonstrated by altering the focussing. Owing to repeated division, there is a rapid increase in the number of the axis cylinders, just like that which has been already described as occurring in the subepithelial plexus of the conjunctiva. The fibres were observed to become progressively finer, and were ultimately lost, after pursuing a long course, and whilst of extremely small diameter, in the substance of the fibrous tissue very near the cartilage. In this course they frequently crossed one another, but never communicated, and thus formed a peculiar kind of plexus; their extremities were marked, not by any increase in diameter, but rather by a diminution, since they simply ran out to a point. Throughout their whole course they were frequently seen to be in contact with the numerous connective-tissue corpuscles distributed through the fibrous bands, but their extremities were never, in spite of the most careful examination, observed to be directly continuous with the processes of the latter.

In the Pigeon and Fowl Helfreich found no traces of nerves having an analogous distribution to those above described in the Frog. Commencing from the plane of insertion of the recti muscles, however, were trunklets running forward throughout the whole circumference of the fibrous capsule; but these, on account of the absence of division, as well as on account of their relations generally, he regarded as nerves that are merely traversing the tissue on their way to the ciliary muscle, iris, cornea, etc. They had a similar destination in the sclerotic of the Mouse and Rat, in which animals the procurement of good specimens was rendered very difficult on account of the manifold and intimate connections between the sclerotic and choroid.

At the same time the anterior distribution of the ciliary nerves was here very clearly brought into view. In his observations on the sclerotic of the Rabbit he always selected young albino animals, and here found that, quite in correspondence with the relations of the nerves entering the sclerotic of the Frog, there was a primary expansion of exactly the same kind, and a single division of the trunks, which were then speedily lost. The whole appearance of this expansion was nevertheless so similar to the type of that above described in the Frog, that he had no hesitation in regarding the latter decisively as composed of nerves destined for the fibrous membrane; and he had as little doubt that in the same animals the conjunctival nerves terminate immediately beneath the epithelium, although they only stain with gold as far as to the axis cylinders.

IX.

THE LACHRYMAL GLANDS.

By FRANZ BOLL.

General Structure.—The lachrymal glands of Man and Mammals agree in all essential points of structure with the salivary glands (see chapter xiv., vol. i.), and belong, therefore, to the so-called acinous type of glands. Like the salivary glands, they are subdivided by a richly developed system of frequently decussating septa, which are given off from the capsule, and dip into the substance of the organ, into a number of polyhedric bodies of the most diverse form, but in general of tolerably constant size; and these septa, when examined under the microscope, are seen to be composed of loose fibrillar connective tissue. The principal portion of the polyhedric bodies, which in a strict sense we would characterise as the proper parenchyma of the gland, is seen in transverse sections to be almost exclusively composed of alveoli and bloodvessels. It is only in rare instances that we are fortunate enough to exhibit in one and the same section of a parenchymatous body the excretory duct together with the accompanying vessels and nerves. All these structures, the trunks of which enter at the hilus of the gland, run collectively imbedded in the loose connective tissue of the septa, from whence they branch off usually at right angles into the parenchymatous bodies, accompanied for a short distance only by connective-tissue fibrils. Apart from these remains of the so-called interstitial tissues, the acini themselves contain no fibrillar connective tissue.

2. The Alveoli.—The form and dimensions of these bodies,

which form the proper secreting parenchyma, present but slight variations. They form sacculi, in which we can distinguish an investing membrane (membrana propria), and the secreting epithelium.

The epithelial cells are of very various shape, but form polyhedric bodies of nearly equal size, that are bounded by a variable number of surfaces which come into apposition at different angles, but almost always have sharply defined borders.

Not unfrequently tolerably well-defined delicate grooves are met with upon the surfaces. None of the different diameters of the epithelial cells are especially developed at the expense of the others, so that they invariably appear in the form of irregular cubes. The spheroidal homogeneous nucleus, not always containing well-marked nucleoli, is in all instances excentric, being situated near the base of the cell which is turned towards the membrana propria. A tolerably strong and long bright process, staining deeply with carmine, is, it would appear, constantly given off from the cell (Heidenhain), which seems to end by a free extremity at some distance from the cell, without forming any other connection. Its length may almost amount to the diameter of the body of the cell. The other angles of the cells are not unfrequently drawn out into long processes, the size of which is usually considerably less than that of the basal process. Not unfrequently, also, the nucleus of the cell exhibits a pointed process, which can never be followed beyond the limits of the cell, but which constantly runs in the direction of, and is sometimes contained within, the basal process itself.

As Henle first demonstrated, and as Heidenhain has lately again pointed out, the acinous glands are divisible into those which contain mucus in their secretion, and into those in which it is absent .Certain histological characteristics of the secreting parenchyma correspond to these peculiarities of the secretion, especially in regard to the glandular epithelium, which, when no mucus is present, constantly remains protoplasmatic, whilst when it is present, the protoplasm undergoes a metamorphosis into mucus that is very easily demonstrable under the microscope. The lachrymal glands of Man and the other animals examined, as the Sheep, Ox,

and Horse, belong to the second kind. In the parenchyma of these glands not a single cell that has undergone mucous degeneration can be demonstrated. It may therefore be concluded with certainty that the secretion of the lachrymal glands never contains mucin.*

According to the researches of Heidenhain, the so-called lunula, first described by Giannuzzi, is formed by a collection of protoplasmatic cells, usually appearing sickle-shaped on section, which are perhaps destined to supply the glandular epithelium that undergoes the mucous metamorphosis. It is obvious that as the lunula is only present in glands in which a mucous degeneration of the secretory elements occurs, we could not expect to meet with a lunula in the lachrymal gland, the cells of which, like the epithelial cells of the submaxillary gland of the Rabbit, remain permanently protoplasmic.

The alveoli are invested by a fine membrane, the so-called membrana propria, the structure of which is very peculiar. It is always composed of flat stellate cells, which frequently intercommunicate by means of their often very largely developed processes, that run round the alveoli like hoops. These finely striated, more or less slender or broad processes which constantly lie flat on the curvature of the alveolus, proceed from the nucleated central portion of the cell; they do not however form an interrupted investing membrane like basket-work to the alveolus, but appear in the form of thickened striæ and ribs in a membrane firmly surrounding and enclosing the alveolus, composed of these stellate cells in a manner of which it is not very easy to give a clear description. The cells and their processes, in their relation to the substance of the membrana propria, may best be compared to the ribs of a leaf, or with toes between which a swimming membrane is expanded. We cannot however draw a completely sharp line of distinction between the ribs and the substance of the membrane, or show

* The only analysis of the tears of Man hitherto published, that by Frerichs (in the article 'Tears,' in Wagner's *Handwörterbuch der Physiologie*, Band iii., Abtheil i., p. 618), certainly admits the existence of a small quantity of mucus. But in this instance the secretion of the Meibomian follicles was not excluded.

that these stellate cells are anything different from the membrane. The whole thing constitutes an histological unity; the stronger longitudinally striated ribs are distinguishable from the matrix of the membrane, but pass quite gradually and imperceptibly into the matrix, which last, usually on both sides of the ribs, becoming gradually fainter, exhibits a longitudinal striation parallel to the ribs.

This description of the structure of the membrana propria, the correctness of which may be easily established by the examination of preparations of glands treated with iodine-serum and teased out with needles, or of sections of glands cautiously hardened in Müller's fluid and brushed out at their free borders, forms a most satisfactory explanation of the extremely various appearances which frequently occur in the same preparation, according to the more or less prolonged maceration to which it has been subjected, or the greater or less facility with which the tissue breaks down. Owing to these causes, appearances may be obtained from the teasing out of glands macerated in diluted Müller's fluid of a variable and, as it would almost appear, a completely contradictory nature. Sometimes isolated alveoli are met with, the epithelial cells of which appear to be contained in a perfectly closed and for the most part strongly wrinkled homogeneous sac; sometimes, on the other hand, there are naked groups of epithelial cells which still preserve the form of the alveoli, and to which a few isolated stellate cells adhere. Then, again, perforated basket-work masses, composed exclusively of stellate cells and their processes, float in the fluid, and in the cavities of these a few secretory epithelial cells are usually discoverable. In addition to an innumerable number of isolated gland cells, isolated cells are also to be found of the same kind as those that form the membrana propria. The form and size of these are subject to considerable differences. In young animals (as may best be seen in the Calf) they are of larger size, not only in regard to the central mass, but their processes are more developed. Each cell is gibbous in form, the centre being sometimes protruded in the form of a vesicle; and thus, when seen in profile, it often appears like a sickle, which in sections of the hardened gland not unfrequently encircles

the alveolus. If the fluid be moved by pressure on the covering glass, the transition of such a crescentic cell into a stellate multipolar cell may often be observed under the microscope. In young animals a small quantity of granular substance occupies the centre of the cell, surrounding the usually round nucleus, which contains no distinct nucleolus. In older animals this small remains of protoplasm has almost entirely disappeared. The substance of the flat, frequently quite ribbon-like processes is pale, and sometimes finely longitudinally striated. They divide dichotomously at more or less acute angles, and not unfrequently a thick process may be seen suddenly breaking up into several branches.

Some of the processes of these stellate cells penetrate, as may also be shown in isolation preparations, between the epithelial cells of the alveolus themselves. It was maintained by Pflüger, who first accurately examined them in the salivary glands, that these processes are directly continuous with the processes of the secretory epithelial cells, and that from this connection with true epithelial structures the nervous nature of the stellate cells can be demonstrated. Although I am in possession of numerous specimens in which at first sight there appears to be a direct continuity between the two cells, I have not been able to satisfy myself that such a connection really exists.

3. THE INTERSTICES OF THE ALVEOLI.—Whilst the inner surface of the membrana propria is lined by the epithelial cells of the alveolus, the external surface remains free, and during life forms the boundary of a space filled with lymph, which, in the case of each parenchymatous body of the gland, occupies the interval between the external wall of the capillaries and that of the alveoli, and the presence of which can be rendered evident by the most diverse methods, as by simple puncture injections, or by the production of artificial œdema in the gland, in Ludwig's method.

The form and extent of these spaces in the secretory parenchyma must obviously be extremely complicated. In sections of the several parenchymatous bodies, when injected, which is best accomplished with cold fluid Berlin blue, each alveolus of the gland, without exception, appears to be surrounded by a

coloured ring. The alveoli themselves, uncoloured by the injection, lie separately on a coloured ground, an appearance that is often repeated with perfect regularity over a surface presenting forty to fifty alveoli. If the bloodvessels have been coincidently injected with a different colour, as, for example, with vermilion, their irregular peculiarly inconstant division and red colour form a striking contrast to the very regular disposition of the system of canals injected with blue. In fine sections, the bloodvessels, running in the form either of straight or tortuous red lines, or, when seen in section, of red points only, are invariably surrounded by a blue-coloured space, identical in fact with that which surrounds each individual alveolus. These appearances, repeated with unvarying regularity in every section, admit of no other explanation than that an extraordinarily rich, freely intercommunicating system of fissures traverses the parenchyma of the entire gland, surrounding every alveolus and every bloodvessel. It is not that there is a separate sheath for each alveolus and bloodvessel, constituting a peri-alveolar or perivascular space, but a single, continuous, very complicated cavity surrounding every parenchymatous body, which completely separates the bloodvessels from the alveoli, and which everything that the blood brings to the secreting parenchyma must first traverse before it can enter into the secretion.

The already extremely complicated histological and topographical relations of this cavity are rendered still more complicated by the circumstance that a very rich system of various-sized fibres, as well as of stellate cells, is stretched in its interior between the alveoli. On sections of the hardened gland these cells and their processes may be very easily demonstrated. They are to some extent in relation with the stellate cells composing the membrana propria, whilst a few processes also run out to adjoining alveoli, fastening and attaching the walls more or less intimately together. Not unfrequently also cells are found which, lying between two alveoli, belong as much to the investing membrane of the one as the other, sending their processes into both. Cells are also frequently found lying almost perfectly free between the alveoli, or connected only very loosely by means of their processes. It is remarkable that these inter-

stitial connective-tissue cells join only with the external wall of the alveoli, and never with the capillaries, which do not in any instance possess a membrane corresponding to an adventitia capillaris.

Giannuzzi, the discoverer of this lacunar cavitary system in the secreting parenchyma, regards it as a true lymphatic space; that is to say, as standing in direct connection with, and injectible from, real lymphatics, and as analogous with the spaces stated by Ludwig and Tomsa to surround the canaliculi and bloodvessels of the testis, the injection of which can actually be accomplished from the lymphatics of the cord. This, however, has certainly not yet been satisfactorily effected in the case of the above-described space. Numerous attempts failed in consequence of the delicacy of the lymphatics emerging from the glands, and the resistance presented by their valves. Yet appearances are not unfrequently presented in specimens made by simple puncture injections, which at least render it probable that the spaces in the several parenchymatous bodies are in direct communication with true cylindrical lymphatics running in the loose connective tissue of the fissures separating the several parenchymatous bodies. In what mode, however, the cavity situated within the several parenchymatous bodies, and here sharply defined by the external surface of the membrana propria and of the blood capillaries, is shut off towards the larger trunks of the excretory ducts and bloodvessels, as well as towards the connective-tissue septa, has not as yet been clearly demonstrated.

4. THE EXCRETORY DUCTS.—The lachrymal ducts are lined by a single layer of low columnar epithelial cells. Where they enter the gland they speedily break up into numerous branches, which have a similar low columnar epithelial lining, and from these again are given off those ducts that Pflüger has termed "salivary tubes" in the case of the salivary glands, and which may be most appropriately termed lachrymal tubes. Their internal diameter is usually small, and they are lined by elongated columnar cells, which are characterized by presenting a very distinct fibrillation at their basal extremity, which Pflüger has described at great length, and has brought into

connection with the regeneration of the gland tissue. Lastly, from these tubes, lined by tall columnar cells, richly fibrillated at their base, and which appear to be present in all similarly constructed acinous glands, fine canals are given off either by gradual or sudden transition of the epithelium. The canals are not much thicker than capillaries, and present characters which, both in regard to their size and in the dimensions of the cells composing the simple epithelial tubes, are similar to those of all the allied acinous glands. These cells are always much flattened, and are usually characterized by the presence of very substantial processes, which give them a fusiform appearance, or some form analogous to a spindle. They lie with their long axis parallel to the axis of the epithelial tube, and are frequently arranged in an imbricated manner. The canals are finally connected with the alveoli by means of short branches, which, being formed for the most part of from four to six epithelial cells, are prolonged into the interior of the alveoli, where they are invested almost circularly by the peculiar secreting epithelial cells. These last, and still more the former, cells of the excretory ducts, occupying almost the centre of the alveolus, penetrate by means of their processes between the secreting epithelial cells, and have been named by Langerhans (in the pancreas) '*centro-acinar*' cells.

Whilst formerly a very simple form was attributed to the cavity situated in the interior of the alveolus, into which the secreting epithelial cells poured their secretion, investigations undertaken with improved methods of injection by Giannuzzi, Langerhans, Ewald, and Saviotti, have shown that the simple short and minute excretory duct of the alveolus breaks up into a very rich, much branched, and frequently anastomosing plexus of extremely fine cylindrical canals, which, in exactly the same mode as that given by Hering of the relations of the finest biliary ducts to to the hepatic cells, invests the individual epithelial cells, and includes them in its meshes. The canals lose their proper membrane, and beyond this point merely form sparingly distributed ducts situated between the variously formed polyhedric gland cells, which are in close apposition with each other, and are provided both along their borders and surfaces with grooves.

5. THE NERVES.—The nerves of the lachrymal glands run constantly by the side of the branches of the bloodvessels and the excretory ducts. They are, even in the trunk of the lachrymal nerve, for the most part non-medullated. I have never been able to follow them quite satisfactorily beyond the salivary tubes, which they constantly accompany, and I can state nothing with certainty in regard to their termination or their anatomical relations to the secretory elements. No nerves exist in the interior of the parenchymatous bodies in the interstices between the alveoli; and if they are really in direct connection with the secretory epithelial cells, they must run to the alveoli with the finest excretory ducts.*

6. LITERATURE.—The histological literature of the lachrymal glands is identical with that of the acinous glands. Passing over the older works, I subjoin the complete literature since the important researches of Giannuzzi on this subject, which were made in Ludwig's laboratory, and the coincidentally made, and not less important, works of Pflüger.

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* The appearances which I have indicated in my first work, where non-medullated nerves run to the blunt end of the alveoli, can only occur at the margin of the parenchymatous body opposite the connective-tissue septa.

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CHAPTER XXXVII.

UTERUS, PLACENTA, AND FALLOPIAN TUBES.*

I.—UTERUS.

BY DR. R. CHROBAK.

THE peritoneum, which forms an extremely delicate membrane investing the uterus, reaches on its anterior surface a little below the constriction corresponding to the os internum, and on the posterior surface as far as to the attachment of the wall of the vagina to the cervix uteri.† Separating from it at these points, it forms the excavatio vesico- and recto-uterina. Anteriorly as well as posteriorly it is firmly connected with the muscular tissue of the uterus by compact connective tissue, and is so attached that the boundary of that portion which covers the anterior surface, and which can only be detached with difficulty, if at all, forms an angle opening upwards, the apex of which is approximatively in the centre of the anterior surface of the uterus.‡

Laterally the intimate attachment of the peritoneum to the uterus only extends to about the distance of one centimeter below the Fallopian tube; beyond this point the peritoneal laminæ separate from each other in order to permit the blood-vessels, lymphatics, and nerves to gain entrance into the substance of the uterus.

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* The microscopic researches for this essay were made in the Physiological Institute of Vienna.

† Luschka, *Anatomie*, Band ii., p. 360.

‡ Henle, *Anatomie*, Band ii., p. 486.

The principal portion of the substance of the uterus is composed of unstriated muscular fibres which are simply superimposed on one another in a succession of layers; but since even in the pregnant uterus it is not practicable to dissect off the several layers separately, considerable confusion prevails in regard to their arrangement and subdivision.

If the development of the layers be followed, we may reduce the number of layers to three; an internal, chiefly consisting of circular fibres; a middle, in which the fibres run for the most part longitudinally; and an external accessory layer.

The external layer, which is situated immediately beneath the peritoneum, and is intimately connected with it, is by far the thinnest, but at the same time is the most distinct and independent; it is prolonged upon the adnexa of the uterus. This external layer is chiefly formed of a fasciculus of longitudinal fibres on the posterior wall of the uterus arising from the margin of the cervix,* though these fibres pass to enter into its formation from the sides of the uterus, and it then spreads over the organ as far as to the round ligaments.

The second layer, separated from the foregoing by many transverse fasciculi, is composed of numerous strong muscular fasciculi,† extending from behind forward over the fundus; and these again, diverging anteriorly and posteriorly, decussate frequently with other short fibres. Near the middle of the fundus this muscular layer fuses to a certain extent with the superficial one.‡ Beneath this, which is the last distinctly recognizable layer, and which, like that above mentioned, does not cover the sides of the uterus, are a number of tolerably strong smooth and short fasciculi, pursuing for the most part a circular course, which decussate at the most diverse angles, give off a few processes to the ligaments, and run in such a manner that, speaking broadly, those which are superficial in front dip into the deeper part of the uterus posteriorly, and *vice versâ*.

This layer is by far the most important of all those of which

* Hélie, *Recherches sur la disposition des Fibres musculaires de l'Uterus.* Paris, 1869.

† Pappenheim, *Vorlaufige Mittheilung.* Korn and Wunderlich's *Vierteljahrschrift*, 3 Jahre, Heft. i.

‡ Hélie, *loc. cit.*

the uterus is composed, and is recognized by its remarkably large and, during pregnancy, thick-walled vessels.

The innermost layer, which, according to Luschka,* is to be regarded as the most important of all, since it exhibits traces of the early division of the uterus into two lateral halves, is essentially composed of circular fibres, which, proceeding from the circular fibre layer of the uterine portion of the Fallopian tubes, forms successively larger annuli that meet in the middle line, and not only form the foundation of the body of the uterus, but can be traced into the cervical region, and from thence into the vagina. (The so-called internal and external sphincters of the os uteri belong to this circular fibre layer.) Besides this well-marked circular layer, a triangular layer of longitudinal fibres is present on the anterior and posterior wall of the uterus,† the apex of the triangle being directed downwards; from this delicate muscular fasciculi can be traced into the mucous membrane.

The regular arrangement of the fibres described above is less observable in the cervical region of the uterus,‡ where they are grouped into about three layers (Henle). The circular fibres of the innermost layer of the body form by far the largest middle layer, which is bounded externally by longitudinal fibres that are in great part lost in the vicinity of the bladder, vagina, and urethra, whilst the innermost layer is likewise composed of longitudinal muscular fibres that supply the mucous membrane with fibres, and interweave at the os externum and internum with the circular fibre layers forming the sphincters. According to Guyon,§ the sphincter of the os internum forms an isthmus three millimeters in length.

All these layers of the uterus are for the most part composed of contractile fibre cells, so firmly united into fasciculi and flat muscular expansions by means of a strong cementing material

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* Luschka, *loc. cit.*

† Hélie, *loc. cit.*

‡ Retzius, *Struktur des Uterus*, in Froriep's *Tagesbericht*, in Canstatt's *Jahresbericht*, Band i., p. 64, 1850.

§ Guyon, *Etude sur la cavité de l'Uterus à l'état de vacuité*, *Journal de Physiologie*, Tom. ii.

that it is only with great difficulty that they can be isolated. The fasciculi are again combined together by a large quantity of nucleated connective tissue and a few elastic fibres.

The fibre cells of the uterus, as a rule, are fusiform, and often present very attenuated extremities; in the pregnant condition, however, (besides the formation of new cells,) the contractile elements attain so great a development that their length, instead of 0·045 of a millimeter, becomes 0·660 of a millimeter, and their breadth, which was originally 0·009—0·014, increases to 0·074. Many of the muscular fibres have shovel-like, flattened, and dentated edges. The transverse section of the cells presents a rounded, ovoid, three to five-angled outline corresponding to the several angles seen in surface views.

The cell substance is only unclouded in the fresh condition, and during the first two-thirds of pregnancy; it is at this period translucent, and allows the nucleus, which is never absent, and the granules, which are also constantly present at the two extremities, to be distinctly recognized.*

The nucleus, always single, is elliptical, fusiform, or rod-shaped, and varies from 0·002 to 0·015 of a millimeter in length, and from 0·001 to 0·003 of a millimeter in breadth,† (and these measurements also become nearly doubled in pregnancy.) In the greater number of cases it lies in the ventricose enlargement commonly found near the centre of the cell, but is often also excentric or attached to the walls. The brilliant granules occurring in the nucleus are still a subject of controversy.‡

The measurements above given do not hold for the muscular fibres of all the layers, but only for those which play an important part in the expulsion of the fœtus. The superficial fibre cells are shorter, more slender, and more cylindrical, like the muscular cells of the innermost layer, the length of which only amounts to 0·018—0·034 of a millimeter,§ and which do not present any remarkable hypertrophy during pregnancy.

The *mucous membrane* lining the interior of the uterus

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* Arnold, see this Manual, 1868, p. 192.

† Frankenhäuser, *Die Nerven der Gebärmutter*. Jena, 1867.

‡ Hessling, *Gewebelehre*, 1866. Frankenhäuser, *loc. cit.* Arnold, *loc. cit.*

§ Kölliker, *Zeitschrift für wissenschaftliche Zoologie*, Band i.

terminates at the upper end of the isthmus by a sharply defined border.* In the virgin it presents the appearance of a grey or pale pink membrane having a thickness of from 1 to 1·8 millimeters, but becoming thinner towards the cervix and the orifices of the Fallopian tubes.† Its separation from the subjacent muscular coat is not very distinctly marked, and it cannot in consequence be dissected off in large flakes. Its surface is smooth, except near the orifices of the tubæ, where it exhibits very small folds (small papillæ, Hennig).‡ In health it is covered with a thin layer of a more or less grey, transparent, and rather glutinous fluid, possessing a feebly alkaline reaction, and containing in variable, but small proportions, columnar cells, spheroidal granule cells, secretion of the uterine glands, a few cilia, and very rarely perfect ciliated cells; in older persons, cholesterin, monads, algæ, free fat, etc., may be found. (Donné, Taylor, Smith, Scanzoni and Kölliker, Hennig, Schlossberger, Hausmann, and many others.)

The mucous membrane does not possess any definite connective-tissue framework.§ (Henle states that he has here and there, by pencilling out the tissue, discovered a fine plexus of pale fibres. He noticed this also in specimens treated with alkaline solution). It consists of the tubular glands of the uterus, which we shall immediately proceed to describe, between which are large numbers of apparently free nuclei, having a diameter of 0·006 to 0·008 of a millimeter, of elongated or variously formed polyhedric flattened cells, of fibre cells in every stage of development, of a relatively large quantity of intermediate substance, and of muscular fasciculi running up to the base of the glands from the innermost layers of the muscularis.

The *glandulæ utriculares*, first pointed out by Malpighi,||

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* Virchow, in Froriep's and Schleiden's *Notizen ueber die Bildung der Decidua*, (On the formation of the decidua.)

† Robin, *Mémoire pour servir à l'Histoire anatomique de la Membrane muqueuse de l'Uterus*, *Archives général*, Juillet, 1847.

‡ Hennig, *Der Katarrh*, etc.

§ Henle, *loc. cit.*

|| Malpighi, Opp. 1687, vol. ii., p. 220.

then demonstrated by v. Baer,* Burckhardt,† Eschricht and E. H. Weber,‡ and more recently described by Krause,§ Sharpey,|| Reichert,¶ Bischoff,** and especially by E. H. Weber,†† only present one form in Man, whilst in many animals there are two varieties, though this is still to some extent a moot point.‡‡

They form cæcal tubes of various lengths, usually simple, but often giving off from their centre, or just below this point, two, or rarely several, branched tubes, which are either columnar or somewhat inflated near their extremities, and open into the cavity of the uterus, upon the surface of the mucous membrane. Looking down upon the free extremity, the diameter of the opening of which is somewhat larger than that of the gland canal, the tubes often appear laterally compressed or triangular.§§ They are twisted in the most diverse directions, and even form corkscrew-like coils, so that the total length of the gland tube often considerably exceeds the thickness of the mucous membrane. Taken collectively, however, they preserve a vertical position in regard to the membrane, especially at the lower part of the uterine cavity, and near the openings of the Fallopian tubes, whilst in the upper part of the body, and in the fundus, they assume an oblique and often nearly horizontal position.

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* v. Baer, *Untersuchungen über die Gefässverbindung zwischen der Mütter und der Frucht*, (Researches on the vascular connection between the mother and the offspring.) Leipzig, 1828.

† Burckhardt, *Observationes anatomicæ*, Kas., 1854

‡ Eschricht and E. H. Weber, *Braunschweigen Naturforscher Versammlung*.

§ Krause, *Anatomie*, 2nd edit., Band i.

|| Sharpey, see Canstatt's *Jahresbericht*, 1843, Band i., p. 106.

¶ Reichert, Müller's *Archiv*, 1843.

** Bischoff, *Entwicklungsgeschichte der Hunde-eies*, and Müller's *Archiv*, 1846.

†† Weber, E. H., *Zusätze zum Baue und der Verrichtung der Geschlechtsorgane*, 1846, (Additions to our knowledge of the structure and disposition of the sexual organs.)

‡‡ See Sharpey, *loc. cit.*; Ercolani, *Giamb. delle glandule otricolare*, etc., 1868; and Friedländer, *Untersuchungen über den Uterus*, 1870.

§§ Hennig, *Katarrh der weibliche Geschlechtsorgane*, 1870.

The substance of these glands can only be isolated with great difficulty in the healthy uterus. It is more easy to effect this during menstruation and pregnancy, though, on account of their numerous curvatures, it is very rarely that they can be seen throughout their whole length. They are composed of an extraordinarily thin structureless membrane, in the substance of which, especially in the menstruating uterus, elongated oval nuclei are found, which are easily distinguishable from the muscle-nuclei that remain attached to the walls of the gland tubes when they are isolated.

In regard to the epithelium of the glands, I shall here, in consequence of its importance, quote entire the account given by Gustav Lott.*

As early as 1852, Leydig† made a communication in reference to an observation by Dr. Nylander, to the effect that the epithelium of the uterine glands of the Pig was a ciliated epithelium.

Leydig, however, although at the end of this communication he stated as his opinion that similar epithelium might be found in other Mammals and in Man, has not since published any observations bearing on this point.

Kölliker‡ simply corroborated Nylander's discovery. Leydig§ himself, in his Manual of Histology, published five years after the abovementioned communication, again only mentions the Pig; and Frey‖ only does the same in his still more recent work. So far as the literature of the subject was accessible to Lott, no mention of this discovery is elsewhere made. Becker,¶ who investigated the generative organs of

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* See A. Rollett, *Untersuchungen*, Band ii. Leipzig, 1870.

† *Ueber Flimmerbewegung in den Uterindrüsen des Schweins*, (On the ciliary movement in the uterine glands of the Pig,) in Müller's *Archiv für Anat. und Physiologie*, 1852, p. 375.

‡ *Handbuch der mik. Anat.* 1852, Band ii., pp. 445, 446.

§ *Lehrbuch der Histologie*, 1857, p. 518.

‖ H. Frey, *Handbuch der Histologie und Histochemie des Menschen*, 3rd edit. 1870, p. 539.

¶ *Ueber Flimmerepithelium und Flimmerbewegung im Geschlechtsapparate der Säugethiere und des Menschen*, (On ciliary epithelium and ciliary movement in the sexual apparatus of Mammals and of Man,) in Moleschott's *Untersuchungen zur Naturlehre des Menschen und der Thiere*, Band ii., p. 71.

Man and various animals for ciliary epithelium, does not mention the uterine glands at all, and Hennig* was even led to the conclusion, in regard to the glands he observed in the Fallopian tubes, that the principal difference between follicular organs and simple folds of the mucous membrane in the human Fallopian tubes depends on the presence or absence of a deciduous ciliated investment on the mucous surface.

Henle also† expressly states that the columnar epithelium of the glands differs from that of the free surface of the uterine mucous membrane in the absence of cilia.

The other statements in regard to this epithelium are very conflicting. The majority of authors, indeed, ascribe the possession of columnar epithelium to Man and most Mammals, yet not to all. Differences of opinion exist even in regard to Man; for whilst, for example, Weber,‡ Kölliker,§ Leydig,|| Henle,¶ Frey,** and Hennig,†† describe a columnar epithelium, others, as Gerlach,‡‡ Scanzoni,§§ and Schröder,|||| maintain that it is tesselated.

Kölliker expressly terms it an ordinary, Henle and Hennig a ciliated columnar epithelium, whilst Leydig observes "that in all probability the epithelium of the glands exhibits as much ciliary movement as the rest of the internal surface of the uterus."

The statements, again, that have been made in regard to various animals, are not quite in accordance with one another. Leydig¶¶ ascribes to the glands of most Mammals (ciliated?) columnar

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* C. Hennig, *Der Catarrh der inneren weiblichen Geschlechtsorgane* 2 Aufl., 1870, p. 137.

† J. Henle, *Handbuch der systemat. Anatomie des Menschen*, 1866, Band ii., p. 460.

‡ E. H. Weber, *Zusätze vom Bau und den Verrichtungen der Geschlechtsorgane*, 1846, p. 33.

§ *Loc. cit.*

|| *Lehrbuch der Histologie*, p. 487.

¶ J. Henle, *Handbuch der systematischen Anatomie des Menschen*, Band ii., p. 460.

** *Loc. cit.*

†† *Loc. cit.*, p. 13.

‡‡ J. Gerlach, *Handbuch der allgemeinen und speciellen Gewebelehre des Menschen*, p. 352, 1850.

§§ F. Scanzoni, *Lehrbuch der Geburtshilfe*, 4 Aufl., Band i., p. 50.

|||| C. Schröder, *Lehrbuch der Geburtshilfe*, p. 22, 1870.

¶¶ *Loc. cit.*, p. 518.

epithelium. According to Reichert* and Ercolani,† it is a pavement epithelium, which the latter author also maintains is the character of the epithelium lining the glands of the Dog and Mouse. In regard to the Pig, the Ruminants, and Solipedes, most observers agree in stating that their glands are lined by columnar epithelium. Very recently a treatise has been published by Friedländer,‡ in which the author makes mention of the "ciliated columnar epithelium" of the glands of the uterus (p. 25) and cervix (p. 45) in Man, and of the uterine glands in the Dog (p. 55). Friedländer appears to accept these as facts (though they are certainly not generally admitted), without further explanation. This is so much the more remarkable, as we may satisfy ourselves that the exhibition of the cilia of the cells in question is a matter of extreme difficulty in preserved specimens, as will be presently shown, and we are left quite in the dark as to the means by which Friedländer was successful in obtaining distinct evidence of the cilia. It would appear that he must have had preserved specimens under observation, and it would therefore be still more desirable to learn the method he adopted. Moreover, his statement that he observed ciliated epithelium in the cervix of girls not yet arrived at puberty, is not in accordance with observations of many others.

Lott observed ciliary movement in the epithelium of the uterine glands as far as to their fundus, in fresh specimens taken from the Cow, Sheep, Pig, Rabbit, Mouse, and a species of Bat. In four instances, examination of fresh specimens gave a negative result; these cases were those of the Calf, a very young Guinea-pig, a dissected Pig, and a Mare suffering from pyæmia.

In a few cases he observed lively ciliary movement in the epithelium of the gland, when not only had all movement

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* *Ueber die Bildung der Hinfälligen Häute der Gebärmutter und deren Verhältniss zur Placenta Uterina*, (On the formation of the membrana decidua of the uterus, and their relation to the uterine placenta,) Müller's *Archiv für Anatomie und Physiologie*, 1848, p. 78.

† G. B. Ercolani, *Delle glandole otricolare dell' utero e dell' organo glandolare di nuova formazione che nella gravidanza si sviluppa nell utero dell femmine dei mammiferi e nella specie umana*, (On the utricular glands of the uterus and the new glandular organs that develop in the uterus of the female of Mammals and Man.) Bologna, 1868.

‡ *Physiologisch-Anatomisch Untersuchungen über den Uterus von Dr. Karl Friedländer.* Leipzig, 1870.

ceased in the epithelium of the surface of the mucous membrane, but when no cilia were visible.

He states that the best mode of observing the ciliary movement is to carefully break up with needles portions of the membrane excised with scissors, in iodized serum, aqueous humour, or a one per cent. solution of common salt.

The vibrations of the cilia are usually extremely lively, though of very variable duration; in the Mouse and Cat, for instance, ceasing after a few minutes, but persisting under similar conditions under a covering glass, in the Sheep, for an hour or more.

The direction of the strokes of the cilia, as seen in optical longitudinal sections of the glands, is constantly from their fundus towards the orifice, whilst in optical transverse sections a vortex is formed, producing the appearance of a screwlike line.

Observations of the appearances presented at different planes in one and the same tube are easily effected by proper focussing, especially in the Cow, on account of the numerous and often very sharp coils it makes in its course. In order to obtain separate cells with quiescent but well-preserved cilia, Lott spread out a portion of the cornu of the uterus of the Sheep, either fresh or after being kept in iodized serum, in such a manner that he could scrape the surface rather firmly with a convex scalpel without cutting it. By this means the epithelial tubes of the glands can be squeezed out free from all surrounding connective tissue, and the cells may often be seen quite undisturbed in their position. Small fragments of the tube frequently appear in transverse section upon the slide, so that here also the most diverse sectional planes can be looked at coincidently. Such specimens should be examined either in iodized serum, or in a cold saturated solution of bichromate of potash, which renders the cells very transparent, and brings out the nuclei and contour lines with very sharp definition. He never observed vibration of the cilia in such preparations, nor in those macerated in iodized serum, and the quescient cilia had undergone some alterations, yet they were sufficiently distinct to enable him to state that they were extremely short and fine, and that they stood in close apposition to one another.

In sections of uteri which had been macerated in Müller's fluid, or in a four per cent. solution of bichromate of potash, and then in alcohol, he was unable to recognize the presence of cilia, and he was not more successful with those that had been preserved in alcohol, in two per cent. solutions of chromic acid, in a 0·001 per cent. of chloride of palladium, or in a cold saturated solution of bichromate of potash. In such preparations he however always observed regularly closely arranged bud-like elevations on the inner margin of the epithelium, which gave a kind of striated appearance to it.*

Nevertheless it is in hardened specimens that the form and disposition of these epithelial cells may best be studied, especially in very thin sections of preparations that have been hardened in Müller's fluid, and stained with carmine. In such specimens we can also examine in a very circumscribed space all conceivable real and optical sectional planes of the glands, and this whether longitudinal or transverse sections are made through the membrane.

The cells are wedge-shaped, with hexangular cross section, the broad surface looking outwards, and the acute angle towards the lumen of the tube in such a manner that the edge corresponds to the axis of the tube.

In transverse sections of the gland, each cell has the form of an isosceles triangle, with a truncated apex directed inwards. The cells, differing in number with the size of the tube, which varies to a considerable extent, and with the species of the animal, form a ring surrounding the lumen. The narrower the lumen, and the fewer cells form the ring, by so much the more closely does their form approximate that of a triangle; that is to say, so much the smaller is the inner border, and so much the more rapidly do these borders converge internally.

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* In the sixth volume of S. Th. v. Soemmering's treatise "On the Structure of the Human Body," edited by Henle, in 1841, at p. 246, Henle says of the cilia, that "*after death they appear in the form of small spheroidal bodies, and then vanish entirely.*" See also Friedrich on the significance of the striation, in his essay "On the Structure of Columnar and Ciliated Epithelium" in the *Archiv für pathol. Anatomie und Physiologie*, Band xv., p. 535.

The illustrations given by Henle* and Kölliker,† and especially those of the former, correspond to this description; Kölliker only giving a couple of very wide tubes, in which the triangular form is of course a less marked feature. The appearances are differently represented by Hennig,‡ in whose drawing the cells float freely in the lumen of the gland.

In longitudinal sections, on the other hand, the cells everywhere present the form of a parallelogram, with their *long diameter vertical* to the membrane. Lott maintains this in opposition to several authors, who state that the epithelium is of the tesselated or pavement variety. (See, in regard to the Dog, Ercolani; § in regard to the Rabbit, Reichert|| and Ercolani; in regard to the Mouse, Ercolani; and in regard to the human subject, Gerlach,¶ Scanzoni,** and Schröder.†† Lott found the above-mentioned character to be everywhere present, though not with equal distinctness in all animals.

The cells only undergo modifications of form at the points where the gland tubes make sharp curves. In longitudinal sections they here become pointed towards one side, so that on the convex side of the tube their pointed extremities are directed inwards, and on the concave side outwards.

By means of corresponding changes of the focal distance we may also obtain a clear image of the cell boundaries on the external and internal surfaces of the tubes, and thus complete our conception of the form of these cells. On their external surfaces the cells form a beautiful mosaic of tolerably regular hexagons (the bases of the wedges), whilst the internal surface exhibits a similar mosaic of hexagons elongated in the direction of the length of the tube, but appearing very slender in its transverse diameter (the acute border of the wedge). Such a mosaic is most distinctly seen in specimens preserved in Müller's fluid.

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* *Loc. cit.*, figs. 538 and 539.

† Kölliker, *Handbuch der Gewebelehre*, 5th edition, 1867.

‡ *Loc. cit.*, Taf. iii., fig. 10.

§ *Loc. cit.*

|| *Loc. cit.*

¶ *Loc. cit.*

** *Loc. cit.*

†† *Loc. cit.*

Lott found the nucleus, which is usually of very large size (especially in the Dog), and always single, lying without exception in the external portion of the cell, as Henle * and Kölliker † also depict it, whilst Hennig ‡ describes it in Man as lying in a frequently clavate enlargement of the inner extremity of the cell, which Lott never observed. He however here and there found the nucleus so large that one portion of it projected into the internal segment of the cell. When fresh, it appeared coarsely granular, and much more highly refractile than the finely granular dull protoplasm.

The cuneate cells bear the cilia on their slender internally directed extremities. Lott however is unable to state positively whether they occur indiscriminately on all cells, though he regards this as being highly probable, both on account of the constancy of the form presented by the cells, and on account of the invariable presence of the bud-like projections described above, which he considers to constitute the remains of the cilia.

In addition to the animals already mentioned the uteri of other Mammals (as of the Cat, Dog, sexually mature Guinea-pig, Horse, and Man) were examined in hardened preparations, and the agreement of the epithelial cells in all the characters mentioned above established.

The epithelium of the mucous membrane undergoes perpetual replacement;§ and it is more than probable that the epithelium is newly formed after each menstruation.

That uncommonly rapid and uninterrupted changes take place in the epithelial structures of the uterus, is shown by the fact that the relative thickness of the parts composing the mucous membrane varies to an unusual extent according to its stage of development.

In the normal state the mucous membrane measures from one millimeter to 1·8 millimeter in thickness, but at the menstrual period from four to six millimeters; the glands which in the normal uterus are separated from one another by a

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* *Loc. cit.*

† *Gewebelehre.*

‡ *Loc. cit.*, p. 13.

§ Kölliker, *loc. cit.*

space of 0·03 to 0·1 of a millimeter, approximate at this period so closely that only quite narrow folds of the membrane intervene between them; and their length, which ordinarily amounts at most to two millimeters, then rises to as much as seven millimeters; their diameter in like manner increases from 0·05 of a millimeter to 0·1, and after conception to 0·240 of a millimeter; and even the epithelial cells which cover the mucous membrane and line the glands, and which in the normal state are from 0·015 to 0·04 of a millimeter in height, attain more than double this size in menstruation and pregnancy.

The mucous membrane of the cervix, which is separated from that of the body by a sharp line of demarcation, is much denser, firmer, and more transparent than that of the fundus. Its thickness varies from 0·25 to 3·00 millimeters. A special connective-tissue layer is found in the posterior wall between the mucous membrane and the muscular tissue. This layer extends over the os internum as far as to the body of the organ.*

The internal surface of the cavity of the cervix covered with mucous membrane, shows upon its anterior as well as upon its posterior wall the well-known *plicæ palmatæ*, forming branching arborescent ridges, of which the anterior are placed somewhat to the right, and those of the posterior wall somewhat to the left.† The substance of these ridges is composed of a dense tissue containing numerous connective-tissue corpuscles, a few muscular fibres, and a sparing amount of elastic fibres.

The so-called "*mucous follicles of the cervix*" are imbedded in the substance of the ridges, excepting only in the lowermost smooth part of the cervical cavity.

These sacs are usually spheroidal or flattened laterally, or, when partially filled, pressed together in a folded manner. Their size varies according to the thickness of the mucous

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* Rokitansky, *Lehrbuch der pathologische Anatomie*, Band iii.; and Klob, *Pathologische Anatomie der weibliche Sexualorgane*, 1864.

† Hjalmar Lindgren, *Studier ofver lifmodrens byggnad hos menniskan*, Canstatt's *Jahresbericht*, 1867, Band i., p. 25.

membrane, and they open on the free surface by orifices having a diameter of from 0·1 to 0·3 of a millimeter, or by a short broad excretory duct, through which their transparent, colourless, slimy secretion, which possesses a strong alkaline reaction, and coagulates in alcohol, is discharged. Friedländer states that cup cells are present in this mucus. The statements made by the same author, to the effect that there are two kinds of glands, may be reduced to this, that the extremely small mucous sacs of the cervix in childhood become in the adult, by the growth of the mucous membrane, drawn out into tubules, and are still further elongated by their own growth at puberty. They are composed of a structureless membrane, which is so intimately fused with the connective tissue and the muscular fibres extending to the glands, that it is impossible to isolate it.

The glands are lined by a nearly cubical epithelium, the nuclei of which are situated nearer the wall than the lumen.

In the lower half of the cervix the mucous membrane between the gland-openings presents delicate slender papillæ, 0·2 of a millimeter in height, covered with a ciliated epithelium, and each containing a vascular loop.*

Hjalmar Lindgren mentions in addition a thin layer destitute of cells situated immediately beneath the epithelium, which is traversed by processes of the connective-tissue corpuscles.

The epithelium of the mucous membrane lining the cervix is either throughout its whole extent, or only in its upper two-thirds, an actively moving columnar ciliated epithelium, the cells of which often appear to be filiform at their parietal extremity (Friedländer). Towards the os uteri externum it becomes, after exhibiting all the transitional forms, a simply laminated pavement epithelium.

In addition to the above-described mucous glands, closed, colourless, and transparent or sherry-coloured vesicles—*ovula Nabothi*—are constantly met with, though varying in numbers and distribution, and extending in some instances as far as to

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* Kölliker, *Gewebelehre.* Hennig, *Catarrh der weibliche Geschlechtsorgane.* Tyler Smith, *Med. Chir. Transact.*, Vol. xxxv.

the outer surface of the vaginal portion. These have a diameter of from 0·3 to 0·5 of a millimeter, and often reach into the muscularis. They are considered to be partly primary neoplastic formations, and partly retention cysts. (Rokitansky,* Förster,† Hirsch,‡ Kölliker,§ Virchow,|| and others.)

In pregnancy, and during the catamenial period, the mucous membrane of the cervix also shares in the general increase of thickness. The ridges disappear in proportion as the mucous sacs, which then attain a length of from 1· to 2·75 millimeters, enlarge, so that nothing remains of the mucous membrane except a thin trabecular framework three millimeters in thickness, whilst the mucous glands, the epithelium of which becomes larger and more succulent, secrete the consistent mucus that in pregnancy closes the os uteri. On the external surface of the vaginal portion of the cervix, neither folds nor glands are present. The glands of the portio vaginalis, described by Robin¶ and Wagner,** have not, at least in the healthy woman,†† been observed by others; on the other hand, the mucous membrane possesses a great many simple or compound papillæ, each about 0·5 of a millimeter high, each containing a single vascular loop, and each invested with, in many instances, as many as ten layers of epithelial cells. The epithelium itself, very easily separable as a whole, is composed of columnar cells in its deepest layers, which become above flattened, clavate, elliptic, and spiny, till in the most superficial layers they only constitute small thin laminæ connected by a relatively large quantity of cement.

The *nerves* given off from the cervical and adjoining ganglia, and from the plexus hypogastricus, enter at the lateral border of the cervix, and by the ligamentum latum, in a horizontal direction, into the muscularis, and spread themselves horizon-

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* Rokitansky, *loc. cit.*

† Förster, *Handbuch der allgemeine pathol. Anatomie.*

‡ Hirsch, *Ueber Histologie und Formen der Uteruspolypen. Dissert. inaug. Giessen*, Canstatt's *Jahresbericht*, 1855, Band ii.

§ Kölliker, *op. cit.*

|| Virchow, *Krankhafte Geschwulste*, Band i., p. 264.

¶ Robin, *Gazette des Hôpitaux*, 1852, 11.

** E. Wagner, *Archiv für physiologische Heilkunde*, Band xv., p. 495.

†† Friedländer, *loc. cit.*, p. 47.

tally, without in all instances following the course of the vessels to the anterior and posterior surfaces of the organ. Upon the whole, the cervix, in which nerve fibres may be followed as far as to the mucous membrane, appears to contain more nerves than the body (Kilian); * on the other hand, the fundus uteri appears to be more sensitive than any other part of the mucous membrane (Lazarewitsch † and others).

In the uterus, doubly contoured and pale nerve fibres are found, as well as, according to the researches of Frankenhäuser,‡ Koch,§ Kehrer,|| Luschka,¶ Polle,** and others (at least in animals), ganglia in the submucosa, with each of which two or three pale nerve fibres are in connection.

Further classification of the nerves is not at present possible, since their mode of termination in the mucous membrane is not known. Kilian, Polle, and others, certainly describe the entrance of the nerve fibres into the papillæ of the cervix, and Hjalmar Lindgren even finds a fine plexus of pale fibres with intercalated highly refractile and finely granular masses which, breaking up in a brush-like manner, extend to the epithelium. The nervous nature of these fibres is not, however, altogether beyond question.

The distribution of the nerves in the muscular tissue of the uterus has frequently, of late years, been the subject of investigation. According to Frankenhäuser,†† pale fibres proceeding from dark-edged fibres form plexuses around the muscles before they, becoming converted into nucleus- and then into node-bearing fibres terminate in the nuclei of the muscle cells.‡‡

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* Kilian, *Nerven des Uterus*, *Zeitschrift für rationelle Medizin*, 1851.

† Lazarewitsch, the *Lancet*, 1867, No. 17.

‡ Frankenhäuser, *Jenaische Zeitschrift*, 1864, Heft. i.

§ Koch, *Ueber das Vorkommen von Ganglienzellen an den Nerven des Uterus*, (On the presence of ganglion cells on the nerves of the uterus.) Göttingen, 1865.

|| Kehrer, *Beiträge zur Geburtskunde*, 1864.

¶ Luschka, *loc. cit.*, p. 378.

** Polle, *die Nervenverbreitung in den weiblichen Genitalien*. Göttingen, 1865.

†† Frankenhäuser, *Nerven der Gebärmutter*.

‡‡ Arnold, *loc. cit.*

There is an indubitable growth of the nerves also during pregnancy (W. Hunter, Tiedemann, Remak, and others), and, according to Kilian, the double-contoured nerves may be followed further in pregnancy than in the virgin state.

The *bloodvessels* of the uterus proceed from the arteriæ uterina hypogastrica and uterina aortica (Luschka), and from the arteria spermatica externa. The veins unite to form two plexuses, the plexus uterinus, and the plexus pampiniformis.

The two first-named arteries meet together upon the lateral surface of the uterus, forming an arch from which vessels of moderate size penetrate into the muscular layer, speedily branch, anastomose with the arteries of the opposite side,* surround the muscular fasciculi, and from thence extend to the mucous membrane. They form here, after surrounding the glands with capillaries, an irregular plexus of wider vessels in close proximity to the surface, from which thin-walled veins without valves arise.

A much more regular arrangement of the vessels occurs in the cervix, and they here present disproportionately thick walls, so that the lumen only amounts to about one-third of the total diameter (Henle). Towards the cavity of the cervix the vessels run vertically to the surface in the septa between the mucous glands, and form a very superficial capillary plexus, from which a vascular loop ascends into each papilla. Externally, towards the labia, and extending through the muscularis as far as to the mucous membrane, are delicate, often slightly tortuous, or, in the upper parts, spirally twisted arteries, which form the capillary plexus immediately beneath the epithelium which supplies the papillæ with loops, and from which the returning veins again take origin.

The bloodvessels attain perfectly colossal dimensions after conception, which is principally owing to the hypertrophy and new formation of these contractile elements.

The *lymphatics* form large plexuses in the peripheric layers immediately beneath the peritoneum in the pregnant uterus. The lymphatics proceeding from the body of the uterus ex-

* Hyrtl, *Topograph. Anatomie*, 1860, Band ii. p. 180.

tend to the plexus pampiniformis, in order to meet with the lymphatic glands of the lumbar region, whilst those arising from the cervix run to the lymphatic glands of the true pelvis. The lymphatics in the interior of the uterus are almost unknown.

Hjalmar Lindgren describes the lymphatics in the collum as forming arches, from which cæcal processes with sinuous margins extend towards the epithelium.

Methods of Research.

The coarse fibrillation of the uterus is best studied in the pregnant uterus, either in the fresh state, or hardened to some extent in alcohol, or macerated for a little while in a warmed mixture of 1 vol. of hydrochloric acid and 90 vols. of alcohol. In order to make good sections, the alcoholic preparations may be dried in air, or after previous boiling in dilute wood vinegar.

For the purpose of isolating the muscular fibres, very diluted solutions of chromic acid, containing from 0·1 to 0·01 per cent., may be employed, or solutions of bichromate of potash, iodized serum, potash lye, or acetic acid containing one to two per cent.; twenty per cent. solutions of nitric acid; Moleschott's fluid; a one-half per cent. solution of nitric acid heated to the boiling point; wood vinegar alone, or this mingled with glycerine.

To effect the hardening requisite to display the epithelium and nerves, chromic acid, bichromate of potash, alternately applied or mingled together, Müller's fluid, and freezing, are well adapted; but for the finest branches of the nerves the wood vinegar in glycerine is still the best.

As colouring agents, carmine, anilin, picric acid, chloride of palladium, chloride of gold, may be used.

But by far the most important is the investigation of preparations as fresh as possible, and merely moistened with solution of albumen or iodized serum.

II.

PLACENTA.

This account has been furnished by Dr. Reitz, of St. Petersburgh, who made the investigations bearing upon the subject under my directions.—STRICKER.

THE placenta of the human subject is composed of a maternal and of a fœtal portion; but from the fourth month of pregnancy these are intimately fused together. The maternal portion, the placenta uterina, which upon the average is from a quarter to half a millimeter thick, is composed chiefly of large cellular elements. The cells are very variously formed, and are for the most part thickly granulated, and exhibit a distinct large spheroidal nucleus, with one or several nucleoli; occasionally two or more nuclei are present; many cells are provided with one or several processes of various lengths. Between these cells, large vesicles, with numerous nuclei in their interior, are, according to Kolliker, to be here and there found.*

The cells are usually arranged so closely that they form nearly the whole thickness of the placenta uterina; but they are frequently arranged also in groups, and sometimes also in quite an isolated manner, imbedded in the matrix, which appears as a fibrous tissue, or in parts as a hyaline finely granular mass. Between these cells I† found colossal encapsuled cells with large vesicular nuclei and nucleoli. In consequence of their coarsely granular contents, nuclei and nucleoli, as

* Kölliker, *Entwickelungsgeschichte*, 1861.

† *Sitzungsberichte d. K. Akad. der Wissenschaften*, Mai-Heft. Wien, 1868.

well as their remarkable size and enclosure in capsules, they present a remarkable similarity to ganglion cells.

The presence of *smooth muscular fibres* first described in the placenta uterina by Ecker,* and subsequently by Kamenew,† has been positively denied by all other inquirers. My own researches demonstrate the presence of smooth muscular fibres to be constant in the external layers of the placenta uterina. The fibres are tolerably abundant, and are frequently arranged in a laminated manner in teased-out preparations, which, in accordance with the recommendations of Jassinski,‡ have been treated with hydrochloric acid; a distinct well-defined rod-like nucleus may be shown to exist in many of the cells. In addition a not inconsiderable number of fusiform cells, the characters of which could not be more closely investigated, are visible in the various layers of the placenta uterina.

The processes of the placenta uterina, which like septa bound the cotyledons, and frequently divide and branch, penetrate deeply into the fœtal part, without ever reaching, as Kölliker has pointed out, the innermost part of the fœtal portion of the placenta. No direct passage of these processes into the fœtal tissue exists, but they cease at the periphery of the cotyledons, so that in the centre of the secondary cotyledons (Kamenew) no maternal tissue occurs between the villi. In the finer ramifications of these processes, which resemble fibrous tissue, (the cellular) elements of the placenta uterina are but seldom found.

In reference to the *bloodvessels* of the mature placenta, the researches of Kölliker, Virchow,§ and others have shown that there is no plexus of capillaries between the arteries and veins; but that a communication between these two sets of vessels is established by means of sinuous cavities.

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* Icones' *Physiologicæ.* Explanation of Taf. xxviii.

† *Mikroskopische Untersuchungen der Blutgefässe des Muttertheils der Placenta,* (Researches on the bloodvessels of the maternal portion of the placenta,) *Medicinsky Westnik,* 1864, No. 13.

‡ *Zur Lehre über die Struktur der Placenta,* Virchow's *Archiv,* October Heft, 1867.

§ *Ueber die Bildung der Placenta, Gesammelte Abhandlungen zur wissenschaftliche Medicin.*

These sinuses, which traverse the whole placenta, and project freely into the fœtal villi, are exclusively bounded by the placentary tissues. Kölliker and Bidder* were unable to discover the presence of the thin membrane described by E. H. Weber† as forming an investment to the maternal cavities.

The fœtal portion—the placenta fœtalis—is formed by the development of the villi of the chorion, in which are distributed branches of the two arteries and of the vena umbilicalis.

The villi of the placenta fœtalis have very recently been subjected to renewed examination by Jassinsky. He corroborates the statement that the villi are invested by tesselated epithelium, and he even admits that the cells forming this layer may be covered by columnar epithelium; for inasmuch as the villi project and penetrate into the uterine glands, the columnar epithelium of these glands may still remain adherent to the isolated villi. My own researches upon this point have led to the following results: Some villi really have an investment of columnar cells, but in that case there is no subjacent layer of epithelium. The columnar cells bound the cavity of the villus in which the bloodvessels are contained. The young villi, on the other hand, are invested neither by columnar cells, nor by pavement cells, nor indeed by any well-defined cell bodies. They are rather composed of simple protoplasm, with numerous nuclei imbedded in its substance. The villi, as is well known, shoot out protoplasma-threads or knots from their substance. These elongate, and become thickened, and nuclei accumulate in them; yet there are not here any well-defined cell groups, but merely a coherent mass of protoplasm. A cavity subsequently forms in the villus, but even then no epithelial cell walls can be brought into view by the silver method of staining.

The villus however is soon invested by a layer of columnar cells, formed from this mass of protoplasm containing nuclei. At least, it is only in this way that the successive histological stages and phenomena can be explained. In the

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* *Zur Histology der Nachgeburt*, (On the histology of the afterbirth,) Holst's *Beiträge zur Gynäcologie und Geburtskunde*, 1867, Heft ii.

† R. Wagner, *Physiologie*, 3rd edition.

first instance there are filiform solid villi; these subsequently become thicker, then contain many nuclei, then have a cavity in their interior, and finally have an investment of columnar cells surrounding the cavity.

I must further remark, that I have in many instances seen the border bounding the villi externally, and described by Goodsir * and Schröder van der Kolk † as an independent membrane, raised up and isolated from the matrix; and in such cases I repeatedly saw the nuclei separated from the border by a more or less thick layer of matrix. I do not know whether the limiting membrane exists during life. In fresh villi no double contour is apparent, even when they are examined with the best microscopes. The membrane, which may be found partially detached when Jassinsky's method (maceration in hydrochloric acid) is employed, may also be a product of the coagulation of the superficial layer of protoplasm. It is moreover not probable that a membrane should form upon the threads protruded from the protoplasm, since one is subsequently seen investing the free extremities of the superficial columnar cells.

The vessels of the villi are not in direct contact with the wall of the villus, but rather float in a cavity of the villus, which may thus be termed a perivascular space. This cavity is usually widest at the ends of the villi, and in the villus-protrusions into which the vessels only just enter.

Schröder van der Kolk was the first to demonstrate that the arteries and veins in the villi do not form simple loops, but are connected by a close capillary plexus.

The connective tissue of the chorion penetrates with the vessels into the interior of the villi. On the pedicles of the villi it exhibits a distinctly fibrous structure (Virchow's mucous tissue), but near the extremities of the villi it appears as structureless intercellular substance in which no indications of a fibrous structure are perceptible.

Round, fusiform, and stellate cells are distributed through

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* *Anat. and Path. Researches.* Edinb. 1845.

† *Waarnemingen over het Maaksel van de menschliske Placenta en over haren Bloedsomlook.* Amsterdam, 1851.

this matrix of the villi, which are regarded by Kölliker as formative cells of the connective tissue. Besides these there are also nuclei which have no cell substance around them. The matrix of the villi is directly continuous with the connective-tissue matrix of the chorion.

Between the chorion and the amnion there is still a gelatinous tissue, the so-called membrana intermedia, which, according to Bischoff's* researches, represents the remains of the fluid originally present between the chorion and amnios. No cellular elements or vessels are discoverable in this gelatinous layer.

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* *Beitrag zur Lehre von den Eihüllen des menschlichen Fœtus*, (Essay on the membranes of the human fœtus,) 1834. (Kölliker, Bidder.)

III.

THE OVIDUCTS.

(*Fallopian Tubes.*)

The subjoined description of the Fallopian tubes has been executed by Mr. Grünwald, who has worked under my direction.—STRICKER.

THE OVIDUCT.—The oviduct in Man is attached to the upper and lateral part of the uterus, behind and somewhat above the origin of the ligamentum teres. It runs outwards along the upper free border of the ligamentum latum, which constitutes a kind of mesentery for it,* and is partly straight and partly sinuous. The straight segment (isthmus, Barkow) is near the uterus, the looped part—ampulla (Henle)—is more external.

The course of the Fallopian tubes varies in Mammals. They are sometimes looped immediately after their origin from the uterus, and then run straight towards the ovary, though sometimes the reverse obtains. Sometimes they form a series of small curves along their whole extent, or they are contorted into a knot, and intertwine with one another as in the Rat,† the Simia silvanus, and to a still more marked extent in the Opossum.‡

The tubes are not always of equal length; sometimes the right and sometimes the left is the longer. The isthmus is

* Henle, *Lehrbuch der Anatomie.*

† Meyerstein, Henle and Pfeuffer's *Zeitschrift*, 3 Reihe, Band xxiii., p. 63. *Ueber die Eileiter einigen Säugethiere*, (On the Fallopian tubes of some Mammals.

‡ Blumenbach, *Vergleichende Anatomie*, p. 486.

always shorter than the ampulla, although the relative length of the two varies in different species of Mammals.

In the Fowl, as in almost all Birds, only one oviduct is present, that, namely, of the left side. The rudiments of a pair of female sexual organs are, indeed, originally present, but in the course of development that of the right side usually disappears.* This passes downwards, pursuing a more or less tortuous course in front of the left kidney, to the cloaca. At the lowest part it suddenly dilates, and becomes a uterus. It is fixed in its position by a peritoneal fold.

In Amphibia the oviduct again becomes double. In Bufo cinereus it extends upwards over the root of the lung, and is at this its abdominal extremity, for about eight to ten millimeters, fastened by means of a peritoneal fold to the posterior abdominal wall. The upper part is very tortuous. At the lower end it becomes suddenly wider, and terminates in a vesicular dilatation which directly opens into the cloaca.

The oviduct in Man and Mammals communicates by its narrow ostium uterinum with the cavity of the uterus. In Man this opening is at the upper part of the uterus, and is so small that it will scarcely permit the passage of a fine bristle. It enlarges as it approximates its external orifice—the ostium abdominale—but contracts again at the orifice itself. Haller maintained that after its dilatation it again underwent constriction near its middle, and Weber† held the same opinion. Meckel‡ gives the diameter of the ostium uterinum at half a millimeter, that of the ostium abdominale at three to four millimeters. Krause§ estimates the diameters of the ostium uterinum at one-fifth to one-fourth of a millimeter, and that of the widest portion in front of the ostium abdominale at two millimeters. Huschke‖ gives as much as three to four millimeters for the diameter of the tube at this latter point.

In Man the Fallopian tube dilates to form a funnel at the

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* Stannius, *Lehrbuch der vergleichenden Anatomie der Wirbelthiere*, p. 333.

† Band iii., p. 616.

‡ Band iv., p. 516.

§ Band i., p. 559.

‖ *Loc. cit.*, p. 470.

ostium abdominale, and the margins of the funnel are divided by deep radially arranged fissures into many lobes or fimbriæ, which are sometimes pointed, and sometimes rounded. On the inner surface of these lobes, transverse and longitudinal folds are found, which are prolonged from the mucous membrane of the ampulla, and cannot be removed by stretching. One of the fimbriæ considerably exceeds the others in length. This is the fimbria named ovarica by Henle, which is attached by its peritoneal surface to the sharp and free border of the ligamentum infundibulo-ovaricum (Henle), itself a secondary fold of the ligamentum latum, extending between the lateral extremity of the ovary and the infundibulum. This fimbria ovarica reaches to the apex of the ovary, where its peritoneal investment fuses with the albuginea of the ovary. In many cases, however, it does not extend as far as to the ovary, and the ligament. inf. ovaricum then forms a groove or gutter. In the cases where an intervening space remains between the fimbria ovarica and the ovary, the intermediate sharp and naked border of the peritoneal fold is invested by ciliated epithelium.

In the Fowl a furrow always intervenes between the ovary and oviduct, and I found that in this animal the ostium abdominale offers two relations. In three cases the oviduct terminated cæcally, but presented an oblique incision near the apex, which opened into a thin-walled funnel. The incision was situated in the above-named furrow. This mode of termination, however, occurred in young animals that had as yet laid no eggs. The fourth was an old hen, and in this instance the ostium abdominale was infundibuliform, just as in the human subject.

In Bufo cinereus the abdominal opening is situated at the upper attached extremity in a transverse fold of the peritoneum, and exhibits the same relations as in young Fowls.

A transverse section of the Fallopian tube in Man and Mammals shows that the lumen is stellate, and the following layers may be distinguished from without inwards :—

1. The very vascular adventitia, composed of connective tissue. 2. The muscular layer, chiefly consisting of circular fibres, though longitudinal muscular laminæ are interposed amongst them to a variable extent. 3. Lastly, the mucous membrane, which presents numerous folds that are partly

laminar, partly conical, or form low ridges. The epithelium consists of tolerably high columnar and ciliated cells. The matrix of the folds is a dense, very vascular fibrous plexus. The muscular layer of the mucous membrane is made up of longitudinal muscular fibres.

At the ampulla the adventitia and muscular layer present the same relations, but the mucous membrane is beset with many complicated folds that suggest it has to perform a different function. These folds project farther into the lumen of the canal than in the isthmus, and often appear to, and sometimes actually do, coalesce with those of the opposite side. These folds often have secondary folds upon them, which again branch, giving to the whole an arborescent aspect. Simple unbranched folds also occur, arranged in close apposition with each other, which have led several authors (Bowman, Hennig) to admit the presence of glands in the mucous membrane of the oviduct. It may however easily be demonstrated in longitudinal sections that no glands exist in the oviducts of Man and Mammals.

As regards the minute anatomy of the fimbria, they are composed of the same elements as the other parts of the oviduct, of which they are to be regarded as the direct continuations. They are exceedingly vascular.

In the Fowl the external investing membrane and the subjacent circular muscular layer are arranged as in Man. The folds of the mucous membrane throughout the whole length of the oviduct are unbranched, and consist of a finely fibrillated plexiform tissue, in which cells usually of a rounded form are distributed, and increase in numbers towards the epithelium. In the centre of the fold is a vascular trabecula of connective tissue, which gives off branches on all sides into the substance of the fold, producing by their intercommunications the above-mentioned finely fibrillated plexus. At the apex of the fold the connective-tissue trabecula disappears, having exhausted itself by giving off successive branches into the interior. The epithelium is composed of many tiers of columnar and ciliated cells. The folds vary in length.

The structure of the oviduct in Bufo cinereus is quite different; for whilst in Mammals and Birds glands are never present,

tubular glands arranged vertically are found *throughout the whole length*, with the exception of the upper attached portion, of the oviducts of this species, and they are separated from one another only by thin layers of connective tissue proceeding from the mucous membrane.

If the longitudinal folds of the mucous membrane that are met with throughout the whole length of the canal, and which attain their greatest height near the ostium abdominale, be separated from one another by means of needles, a fine velvety tissue, presenting minute openings, and resembling a honeycomb, may be seen, excepting only at the attached abdominal extremity, where the glands are less numerous.

In transverse sections an investing membrane composed of connective tissue is seen; externally to this succeeds a thin layer of circular muscular fibres, on which the mucous membrane lies. The gland tubes are imbedded in this membrane, and, as already stated, they are only separated from one another by the vascular connective-tissue trabeculæ given off by the tissue of the mucous membrane. The mucous membrane rises above these in numerous longitudinal folds, between which the openings of the gland tubes are visible. The tubes are lined by well-defined pavement cells. The folds of the mucous membrane in Man are moderately prominent, and are frequently branched. Their interior is occupied by a dense cord of connective tissue, in which bloodvessels and a few smooth muscular elements are contained. Externally they are coated by tall columnar and ciliated epithelial cells. In the further course of the oviduct the folds are unbranched.

CHAPTER XXXVIII.

DEVELOPMENT OF THE SIMPLE TISSUES.

BY S. STRICKER.

THE status nascens of a vertebrate animal is occasioned by, and coincident with, the impregnation of the female germ. The fecundated germ is a unicellular organism, which becomes by fission multicellular. When the process of division or fission has reached a certain point, the young cells form layers or laminæ, and from these the different tissues are developed, the various organs of the body being again formed from the union of these tissues; coincidently with the appearance of the laminæ, the differentiation of the tissues begins to take place, and it thus becomes intelligible why the account of the embryonal laminæ is worked at with such care by histologists.

Embryologists also understand by the term "embryonic laminæ" the membranes by which the embryo subsequently becomes invested. These investments, however, do not stand in intimate relation to histogenesis; they are really transitory organs, which, like all other organs, develop from the primary laminæ.

A knowledge of the embryonic investments is therefore a part of the history of development of the several organs and the former cannot be discussed without sketching out the principal features of the latter.

From these preliminary observations the line to be pursued in the following account is self-evident. The embryonic cell

layers will only so far be considered as may be requisite to render the histogenetic processes intelligible.

An account of the unfecundated germ has already been given in vol. ii., p. 192 *et seq.* To this exhaustive treatise I have only to add a few observations in reference to the nomenclature. I shall systematically avoid the use of the expression "formative yolk" (Bildungsdotter) employed by Reichert, and that of "principal yolk" (Hauptdotter) used by His. Both expressions, as will presently be seen, are based upon erroneous assumptions, and as neither can claim the advantage of brevity, there is no good reason for discarding in their favour the word "germ," used by Remak. It will, in consequence of this, be further advantageous to term the investing membrane of the germ (the zona pellucida of Baer), not vitelline membrane (Dotterhaut), but blastoderm, germ-tunic, or investment (Keimhülle). I shall only call this tunic the vitelline tunic or vitelline membrane in those cases where the germ exists together with a vitellus (food yolk, Reichert; secondary yolk, His) within one and the same membrane, as in the eggs of Birds, scaly Amphibia, and osseous Fishes.

It is generally admitted that the fecundated germ is at first destitute of a nucleus.* This fact may best be demonstrated in Batrachia, if a pair of animals *in coitu* be examined, whilst some of the ova have been extruded, and others are still retained in the body of the parent. It may then be shown, either by tearing the fresh eggs in sunder, and examining the contents as they escape with low powers, or by section of the hardened ova, that each of the ova taken from the body of the mother possesses a vesicular nucleus (germinal vesicle), the membrane of which can, when fresh, be divided with needles, with the aid of a lens; in the youngest fertilized ova, on the other hand, no nucleus can be distinguished. This fact is interesting, since it shows that the vertebrate animal begins as a non-nucleated mass. If such non-nucleated Batrachian germs be hardened, there

* Precise statements to the effect that the germinal vesicle is persistent, and becomes transformed into the nucleus of the cleavage cells, has only been made by Johann Müller, in the case of the Entoconcha mirabilis. *Monatsberichte der Berliner Akademie*, September 1851.

may sometimes be perceived, when sections are made, a small cavity, corresponding in size to the formerly present nucleus. According to Remak, this is the nuclear cavity of v. Baer. This expression clearly indicates that on this view the cavity occupied by the nucleus still remains when it has itself disappeared.

If the fertilized germ be placed in favourable conditions, a fresh nucleus speedily makes its appearance in its substance. In regard to this nucleus I can say nothing from my own experience, and it would scarcely serve any good purpose to adduce the concurrent testimony of others. As the ova are usually opaque under these circumstances, it is impossible to see the nucleus when fresh. If all observers have been in such complete agreement in regard to the formation of a new nucleus, this is essentially due to the fact that in the later cleavage products of the germ the nucleus is distinctly visible, whilst it may be shown in addition that it is homogeneous, and has exactly the appearance of an oil drop. Reverting to the fact that the old nucleus disappears, it is thus rendered highly probable that we are here dealing with a new formation.

Before the process of cleavage sets in in the germ, it undergoes certain automatic changes of form. The amœboid movements of the Forella germ have already been described (vol. ii., p. 185). If the freshly deposited ova of Bufo cinereus be attentively watched, it may be seen that it has at first several facettes, and that it subsequently assumes a spherical shape. The occurrence of alterations of form in the ovum of the Bird before the commencement of cleavage, has only been deduced from a comparison in hardened preparations of sections made through germs at various stages of development. Here also attention may be called to the observation first made by Bischoff in the ovum of the Rabbit, that the yolk (germ, Keim) retracts from the zona pellucida before it divides.

Whether the observation in regard to the rotation of the unsegmented germ within the vitelline membrane, recorded in the same place, should also be here mentioned as belonging to these movements,

s doubtful. Bischoff only made the observation in one animal, and since that period nothing has been ascertained in regard to the occurrence of rotation in the unsegmented ovum.*

SEGMENTATION AND THE FORMATION OF LAMINÆ.

(*a*.) In Batrachia. The segmentation of the ova in Batrachia was discovered in the year 1824, by Prevost and Dumas,† and given in full detail by Rusconi,‡ in 1826.

No material is so favourable as the ova of Batrachia for the observation of this process. With the return of the first days of spring the spawn may be obtained in large quantities; and if the ova of various species are investigated, they may be repeatedly examined at intervals varying from a few days to several weeks.

Another advantage is that the cleavage proceeds under our eyes, without the necessity of any interference on our part. It is only requisite to place a spawn chain (Bufo) or a mass of spawn (Rana) in water in a watch glass, and with the aid of a lens the whole process may be conveniently followed. The vitelline membrane is not visible (by direct light) by this mode of examination, and we obtain the impression that the germ itself undergoes cleavage upon its surface. If, however, we place a group of ova in a watch glass, and examine them by direct light with somewhat higher powers (as from forty to fifty linear) we may soon convince ourselves that the transparent membrane takes no part in the cleavage.

The formation of the first grooves in the Batrachian ovum may best be rendered intelligible by taking a ball of modelling clay, and constricting it in the following manner. Place a thread in one meridian, and a second at right angles to it. Tighten the two threads so that the upper third of the spheroid is cut through by them. A third thread may now be placed parallel

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* *Entwickelungsgeschichte des Kaninchens*, (History of the development of the Rabbit,) 1842. At pp. 58 and 59 of this work the reader will find the literature bearing upon the rotation of the yolk.

† *Annales des Sciences*, Sér. i., Tom. ii.

‡ *Developpement de la Grenouille.*

to the æquator, about opposite the junction of the superior and middle third of the axis of the sphere, and this should be made to cut its way completely through. By this means, proceeding from the upper pole, the spherule is divided into four segments, whilst the larger inferior portion of the sphere remains undivided, with the exception of the surface, where the two meridianal constrictions indicate the subsequent divisions.

The formation of these three furrows proceeds gradually. It may occupy, at a temperature of 18°—20° Cent. (64°—68° Fahr.), from three to four hours from the period of the extrusion of the egg from the body of the parent.

Before a groove is definitely formed, the surface becomes wrinkled, and then again smooth, and this change occurs several times consecutively. From the principal furrows numerous smaller secondary furrows proceed, which are only of a transitory nature. Reichert has described these secondary furrows as the furrow crown (Faltenkranz), and Max Schultze* has shown that they are the expression of the movement of the germ.

At the point where the first three furrows cut one another (that is to say, in what would be the upper half of the egg floating in water,) a cavity forms. From my own experience I am unable to say whether this coincides with the nucleus cavity or not. The cavity enlarges owing to the retraction and rounding off of the opposed angles of the segments.

The further process of the cleavage is limited chiefly to the four upper segments. These become smaller by continual subdivision, whilst the cavity increases in size, till ultimately a spacious cavity is formed in the upper third of the ovum (*F*, fig. 399), that may be best comprehended with regard to the subsequent processes that take place in it by the following description. It may be regarded as an apple so excavated in the upper third of its axis that only the rind remains. The lower and larger section of the apple would then be solid, whilst there would be a cavity in the upper segment that is only surrounded by a thin cortex.

We designate the cavity in the ovum of the Frog Baer's

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* *De ovorum ranarum Segmentatione*, 1863.

cleavage cavity; the thin-walled dome surrounding it, and formed of small cleavage elements, or embryonal cells (rind of the apple), the roof (*D*); and the solid inferior half, the floor of the cleavage cavity.

Whilst this cavity is forming, the cleavage of the inferior solid segment gradually progresses, though rather upon its surface than in its interior. Thus it happens that the whole ovum is very soon invested by a mantle of small cleavage segments or embryonal cells. The resemblance to a partially excavated apple is now still more striking.

The rind of the apple corresponds to the mantle of small cells, and the solid substance of the lower part to those remains of the germ which only slowly undergo cleavage, and at the period when the mantle is divided off still consist of very large cleavage masses. The comparison, however, may be rendered complete if a circular piece be cut from the rind of the spherical apple at its inferior pole, so as to expose the flesh; for the progressive division (fission) of the superficial cells does not extend so far as to the inferior pole. At this point a small, and in the first instance irregular, but subsequently circular area (*P*) remains, the centre of which corresponds to the inferior pole, and which is composed of large polygonal facettes.

Whilst the external surface of the mantle of all Batrachian germs at this stage of development is of a dark-brown colour, this area remains whitish if the lower half of the ovum was so from the commencement (Bufo fuscus); or it becomes whitish if the lower half of the fresh-laid egg was brown (Rana temporaria, Bufo cinereus, and viridis).

The large white cells that occupy the floor of the cleavage cavity, and are exposed at the inferior pole (*z*, fig. 399), were termed by Reichert the central vitelline mass (centrale Dottermasse). Remak had already applied the term gland-germ to it (Drüsen-keim), because he had found, in accordance with Rusconi, that in Batrachian ova there was no structure analogous to the vitellus. I cannot accept this nomenclature, because the theory on which Remak arrived at it is not tenable. These cells are not exclusively devoted to the formation of the rudiments of the glands. At the same time they are not laminated cleavage elements from which the various tissues are

developed. On this account I shall term them germ cells (Keimzellen), and also point out that their ultimate destiny has not as yet been ascertained.

At the point where the germ cells are exposed, they are at a very early period sharply separated from the outer brown mantle-zone of smaller cells by a semilunar fissure (N). This fissure is named after its discoverer, Rusconi's fissure.* It subsequently becomes completed into a circular groove, and the now still more perfectly circular and well-defined mass of large germ cells has been named by Ecker† the vitelline plug,

Fig. 399.

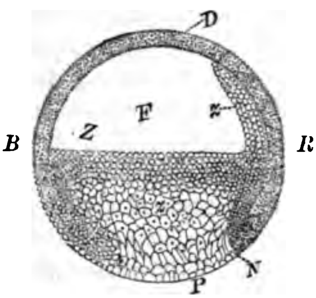

Fig. 399 represents a meridianal section of an egg of Bufo cinereus, the stage of development of which does not quite correspond to that described on this page. *F*, Cleavage cavity; *D*, the roof; *P*, white area at the inferior pole; *Z*, germ cells on the floor of the cleavage cavity; *z*, germ cells which project from the floor of the cavity towards the mantle; *N*, section of Rusconi's furrow; *R*, dorsal half; *B*, abdominal half of the ovum.

(Dotter-propf). I have named that half of the egg‡ where the semicircular furrow commences, the dorsal half, because it forms the dorsum of the embryo; the longitudinal axis of the dorsum runs from the centre of this furrow to the superior pole. The opposite half I have termed the abdominal half.

It was long ago known to v. Baer that the ova underwent in water a rotation of about 90°, so that the meridian became an

* *Developpement, etc.*

† Icones' *Physiologicæ.*

‡ *Zeitschrift für wissenschaft. Zoologie,* Band xi.

æquator. Owing to this rotation the now laterally placed dorsal half is turned outwards. This rotation is occasioned by the formation of a second cavity which extends along the dorsal half. By this means the centre of gravity of the ovum is displaced, and the rotation is a necessary consequence. This second cavity (*N*, fig. 401) was recognized by Rusconi.* Golubew † has by historical inquiry discovered some erroneous references in the nomenclature of the two cavities, and has shown that the cavity of Baer is to be regarded as elliptic, but that of Rusconi as semilunar.

Remak ‡ was of opinion, on theoretical grounds, that the cavity of Rusconi originates from the furrow of the same name by an inversion. He considered that the germ of the Bird is composed of three cell layers or laminæ. The most superficial or most external he named the corneal or sensorial lamina (Hornblatt oder sensorielles Blatt); the second, the middle or motor, or motor-germinal lamina (mittleres oder motorisches, auch motorisch germinatives Blatt), and the third the intestinal glandular lamina (Darmdrüsenblatt). That the Avian germ is laminar, and curves downwards, has been known from the time of C. F. Wolf. Remak believed he could establish the analogy between the Avian and the Batrachian germ by the following observations.

He sought the analogue of the sensory and motor laminæ in the cover or roof of the cleavage cavity; the analogue of the gland-layer of the Bird, on the other hand, in the white area at the inferior pole of the Batrachian ovum. The germ of the Frog, he remarked, is certainly not laminar, and therefore cannot curve inwards in the same manner as the Avian germ. On the other hand, the lower surface of the spherical Batrachian germ undergoes inversion, in order to become applied to the motor laminæ, which he himself, as above stated, believed to be already completed at the inner surface of the mantle layer. I have § however shown that the Rusconian groove is produced

* Müller's *Archiv*, 1836.
† Rollett, *Untersuchungen.* Leipzig, 1870.
‡ *Loc. cit.*
§ *Loc. cit.*

by the separation of the formed elements from one another, and not by an inversion. Proceeding from this groove, I also saw in transverse sections a trace of a division (Trennungs-spur) in one of the mantle surfaces extending upwards in a direction not quite parallel to the dorsal half. I therefore believe I am justified in considering this trace of division as the rudiment of the Rusconian cavity, and in maintaining that this arises not by an inversion, but by a separation of the morphological elements from one another.

In regard to the question whether inversion or fission occurs, Golubew, who is the only author besides myself that has expressed himself definitely upon the point, is in favour of my view. Golubew* however states that my account of the mode of origin of the Rusconian cavity is not quite accurate. I cannot here enter into a controversy upon the subject, because, faithful to my project, I can only so far consider the anatomical details as may be necessary to render the formation of the layers intelligible. In regard to the relations of the fissure to the embryonic laminæ there are no differences of opinion.

Remak noticed that a group of white germ cells projects from the floor of the cleavage cavity, just at the margin where this is continuous with the roof of the cavity, for some distance towards the roof (*z*, fig. 399). I† have further pointed out that this projecting mass of cells is of fundamental importance in the formation of the laminæ.

I have shown that the roof of the cleavage cavity (*D*, fig. 399) contains the rudiment of the sensorial lamina of Remak alone,‡ and that the analogues of those laminæ termed by Remak the middle and gland laminæ, are formed from the cells that are applied as new formations to the roof.

When I found that these germ cells reached at first only a small distance towards the dorsal half, whilst they subsequently extended more and more, until they at length passed beyond the upper pole, the germ cells of the abdominal half at the same time similarly stretching upwards to the roof, and growing towards

* *Loc. cit.*, Taf. D, fig. 2.

† *Loc. cit.*

‡ The same fact has been subsequently pointed out by Götte. See Max Schultze's *Archiv*, Band iv.

them; and after I* had further discovered that the cells of the Batrachian germ were capable of spontaneously changing their form and position on the slide, I stated my opinion that these germ cells strove to pass outwards by spontaneous movements, in opposition to the laws of gravity. Golubew† is unable to adopt this view. He believes that the increase in height is due to cleavage processes.

I am again unable to enter into any discussion in this place upon the different opinions we hold. The question whether the cells move from their position spontaneously, or as the result of progressive fission, is of interest in and by itself, but is of quite secondary importance in regard to the development of the laminæ. It is here only important to notice that the cells generally suffer displacement in order to aid the formation of the embryonal laminæ; and this circumstance may again be regarded as admitted on all sides.

It has been already pointed out that the fissure proceeding from the dorsally situated furrow of Rusconi runs upwards.

When the semilunar fissure in the course of its upward extension reaches the margin of the cleavage cavity, it meets with the above-mentioned white germ cells, which extend along the dorsal half from the floor of the cleavage cavity to the roof. The fissure penetrates these upward extending cells.

If numerous horizontal sections, beginning from the inferior pole, are carried through the ovum, it is found that the fissure existing in the dorsal half is almost semilunar. It is bounded externally by the mantle layer composed of small cells, and internally by the white germ cells (*z*). The mantle zone is at this point much thicker than where it forms the roof of the cleavage cavity. In other words, the fission of the large germ cells to form small ones has at this point progressed towards the axis of the ovum. That which now lies on the exterior of the fissure is no longer the analogue of the sensorial lamina (Remak), but contains the rudiments of all the germ-laminæ. From the fissure a part of the visceral cavity is subsequently formed, and that which lies more externally forms

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* *Ueber die selbständigen Bewegungen, etc., Wiener Sitzungsberichte,* 1863.
† *Loc. cit.*

the whole thickness of the back. Sufficiently thin sections of preparations hardened in chromic acid permit two layers of unequal thickness to be very distinctly seen in this part of the dorsum. The thinner external layer is composed of small cells, and is the analogue of the sensorial lamina of Remak; the thicker internal layer is composed of large cells, but which are constantly becoming smaller than the large germ cells occupying the centre of the floor of the cleavage cavity. From this internal and thicker layer an innermost unicellular layer separates (intestinal gland layer, Darmdrüsenblatt, Remak), whilst the remainder forms the moderately thick middle or motor germinal lamina.

Fig. 400.

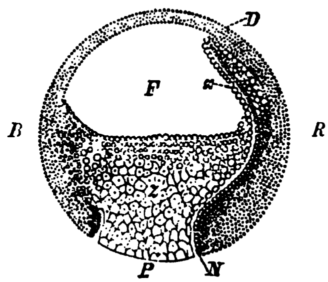

Fig. 400. Vertical enlarged section of an egg of Bufo cinereus. The cavity or fissure proceeding from *N*, and extending to *z*, is, for the sake of clearness, drawn throughout its whole extent as a broad fissure, which, however, in reality only holds good for the upper half; *D*, roof; *z*, floor of the cleavage cavity; *F*, *P*, white area.

The sickle-shaped (as seen on section) mass of cells (*z*) constantly rises towards the pole, and the (in horizontal sections) semilunar fissure extends in the same direction. But as the fissure penetrates into this newly developing mass of cells the portion external to the fissure forms a definite deposit upon the roof of the cleavage cavity, whilst the other part, which is the thinner of the two (*D*) remains as a septum between the fissure (*N*) and the cavity of Baer (*F*).

If meridianal sections dividing the back into two halves be made through ova at this stage of development (fig. 401), it appears that those cells which have reached from the floor of

the cleavage cavity to the roof, and which, after the formation of the semilunar fissure, remain adherent to the roof, are continuous with those cells which were above described as belonging to the internal thicker layer of the inferior segment of the back. In other words, that which subsequently adheres to the roof of the cleavage cavity is the rudiment of the motor and intestinal gland laminæ.

I have already mentioned that in the original roof of the cleavage cavity only the analogue of the sensorial lamina of Remak is to be looked for. This lamina, however, as I* and

Fig. 401.

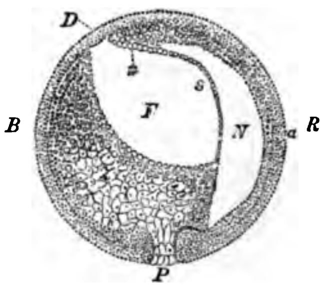

Fig. 401. The illustration here reproduced was obtained from a remarkably successful preparation made in the year 1860. How far it is diagrammatic in its finer details I am unable to say, but the main features are undoubtedly as correct as possible. I have therefore no hesitation in giving it here, notwithstanding that the same relations have been excellently illustrated by Götte, v. Bambeke, and Golubew. My figure appears to me to materially facilitate the understanding of the parts in question, and it is on this account that I give it. The letters *D*, *F*, *P*, *Z*, *z*, as in fig. 400; *a*, dorsum of the embryo; *s*, septum between the food cavity, *N*, and the cleavage cavity.

v. Bambeke† have shown, is composed of two layers in the Batrachia, of a superficial layer of brown cells forming one tier, and of a deeper layer of whitish cells, which in some parts form a single tier, and in others, many tiers. The external brown cells constitute the rudiments of the horny or corneal

* *Loc. cit.*

† *Recherches sur la développement du Pelobates brun, Mémoire publié par l'Academie Belgique,* Tom. xxxiv.

investment of the animal, whilst the inner whitish cells form the proper sensorial lamina.

In Birds and Mammals these two layers are so intimately connected that no difference can be demonstrated between them, even in the most successful transverse sections. Owing to this, Remak has regarded the two rudimentary structures as one, and has designated the whole lamina as the "sensorial lamina" (central portion), or "corneal lamina" (peripheric portion). He has, however, pointed out that there are theoretical considerations that are opposed to the view that the corneal and nervous structures originate in one lamina. The fact is therefore of proportionate interest, that in Batrachia, and, as I shall subsequently show, in Fishes also, the corneal and nervous structures are already distinct at the earliest period of their development. Bearing in mind these circumstances, I apply the term "corneal lamina" (Hornblatt) to the external layer of brown cells, and "nerve lamina" (Nervenblatt) to the deeper whitish cell layer. In regard, however, to Birds and Mammals, and generally speaking, where it has become requisite from later investigations, I shall designate the external germ layer (Remak) as the "conjoined corneal and nervous lamina."

To recapitulate, then, what we have just stated at length, it appears that the corneal and nervous lamina proceeds from an external mantle or investing layer of the spherical ovum, but that the motor and glandular layers originate in the large germ cells collected as a reserve store in the lower half of the ovum. The germ cells have in fact undergone this differentiation in their original position; that is to say, in the lower half of the ovum. But they must be in part also either actively or passively displaced from the inferior towards the superior pole, or, which comes to the same thing, from the caudal extremity of the future larva towards its capitate end.

As soon as Rusconi's groove is completed into a circle, a fissure runs out from its abdominal half towards the upper pole. It scarcely, however, extends as far as one-fourth of the height of the germ cell layer (though its dimensions may vary in different species), and it dilates at the cæcal extremity of the ovum. Remak has termed this cleft the anal cavity.

The cleft first visible on the dorsal half, and appearing semilunar in transverse section, is completed by the anal cavity. If a horizontal section be now carried through the inferior pole, the fissure is seen to be circular. Close to the inferior pole the circle becomes somewhat smaller, and ceases with the freely exposed groove of Rusconi. A funnel-shaped space thus commences at this groove, which is occupied by the plug composed of white germ cells (yolk plug, Dotter-propf, Ecker). As the canal in which the outermost portion of the cone sticks gradually contracts, the white area becomes so small as to be perceptible only as a white point. At a later period this also disappears, and there remains only a canal still recognizable in sections, and with high magnifying powers, which all authors have designated the anal opening. And now, when the extremely attenuated plug of white cells retracts or tears away, (as at least in all probability occurs in Bufo cinereus,) Rusconi's groove communicates with the anal cavity throughout its whole extent. A small annular swelling, visible even to the naked eye, on the outer wall of this cavity, still indicates the point where the yolk plug formerly interrupted the cavity, and the depression in the swelling is a guide to the spot where the section should be carried if it be desired to hit the canal at its *embouchure*.

In the meanwhile the ovum has undergone its rotation; the meridian has become its æquator; the anal opening has a lateral position, the dorsal half being superior, and the abdominal half, with the annulus of germ cells projecting strongly towards the food cavity, being inferior. In the latter, some remains of the cleavage cavity of Baer are long preserved.

The ovum may still be regarded as a vesicle enclosed by laminated walls, except that in the lower half of the vesicle the innermost lamina is pushed inwards by a mass or hillock of germ cells. The various laminæ, however, do not present the same thickness throughout. I must here draw this account to an abrupt conclusion, because these differences already constitute the beginnings of the rudimentary organs, which cannot in this work be further discussed.

(*b*.) THE GERM OF THE FOWL.—In the egg of the Fowl, the

so-called "tread," or cicatricula, constitutes the germ, which is enclosed in the same general investment as the yellow yolk. Pander * described the cicatricula as composed of two easily separable layers, of which one dips into the yellow yolk, whilst the other forms a layer upon its surface. The latter, he says, is a round disk, in and from which the fœtus is formed, and which may therefore justly lay claim to the title of blastoderm (germ-membrane, Keimhaut). The former part was termed by Pander the nucleus of the cicatricula. This is a constituent of the so-called white yolk, which lies beneath, but is not connected with, the central transparent part of the germ-membrane.

Fig. 402.

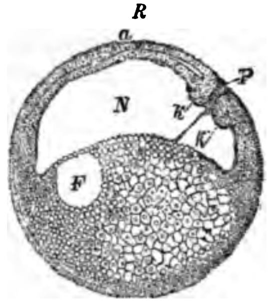

Fig. 402. *F N a P Z*, as in the preceding figures; *k k*, sections of the annular swelling and margins of the anus. The punctated line between *k P*, indicates the antecedent connection of the yolk plug with the germ-cell mass, *z*. The ovum in this condition has already performed the rotation, the dorsum lying above, the abdomen below.

The statement of Pander, that the embryo is developed exclusively from the germ disk, remains unshaken up to this time. Reichert† and His‡ have certainly endeavoured to show, from various points of view, that the morphological elements of the white yolk enter into the new animal body. His, on the ground of his own observations, has also designated the germ disk as the principal germ (Archiblast or Neuroblast), and the accompanying constituent of the white yolk as the

* *Beiträge zur Entwickelungsgeschichte des Hühnchens*, (Essays upon the history of the development of the Fowl.) Würzburg, 1817.

† *Entwickelungsleben im Wirbelthierereiche*, 1840.

‡ *Untersuchungen über die erste Anlage des Wirbelthierleibes*, 1868.

secondary germ (Parablast or Hœmoblast). The account he has given has not, however, been sufficiently proved; and in the course of the subsequent description it will be shown that the observations from which it was drawn permit other significations to be given more conformable to general biological principles.

The account given by Pander refers to the fertilized laid, but not incubated egg. The commencement of incubation certainly cannot be regarded as the beginning of the process of development. During the passage through the oviducts important processes, from my point of view, take place; for the cleavage of the germ occurs here, and the cleavage elements arrange themselves in layers. This lamination has progressed to various stages in different ova at the time of their being laid, and on this account alone it would be disadvantageous to ascribe a definite histological character to this period.

The cleavage of the germ of the Fowl was first described by Coste.* This, however, he did only so far as it can be observed to occur on the surface. Oellacher† examined transverse sections of the yolks of eggs at various stages of cleavage, and in his essay we for the first time meet with an account of the very first traces of the chick. I feel myself compelled therefore to adhere to his statements. But inasmuch as his researches were conducted under my own inspection, the account here given is based in part upon my own observations.

All the preparations here alluded to were obtained by the following means. The yolks of oviducal eggs, or of eggs obtained during the first day of incubation, were carefully freed from albumen, cautiously washed with dilute chromic acid, the albuminous precipitate as it formed being removed with forceps, and the clean yolk then placed in pure diluted solution of chromic acid. After a few days the segment of the yolk containing the germ membrane was removed, and carefully placed in alcohol, where it was allowed to remain till the water was as far as possible removed. It was then imbedded.

* See his *Histoire du Développement des Corps Organisés.*

† Stricker's *Studien*, 1870.

The proper method of imbedding is to make a little paper case, which is then half filled with a mixture of wax and oil.

When the mixture has so far stiffened in the paper case that a preparation laid upon it will not sink in it, the specimen is placed in the desired position, and is again covered with the fluid mixture till the case is full. As soon as this second mass begins to stiffen, the position of the specimen is carefully noted, and when the stiffening is completed, the direction in which the section is to be made is marked. The proportion of the oil to the wax should be so chosen that the consistence of the mixture corresponds to that of the specimen and the convenience of the operator.

I cannot allow this opportunity to pass without expressing my astonishment at the obstinacy with which even excellent microscopists overlook the advantages afforded by such a mixture as the above. The mixture of two bodies of such different consistence as wax and oil enables us to obtain all grades of consistence between those two extremes. For extremely delicate embryological specimens, such advantages are simply inestimable.

I shall here incidentally remark, that where the specimens, as in the case of the ova of Frogs, enclose cavities in their interior, these must be opened to permit them to be filled with the mass. It is only in those instances where the specimen and the mixture of wax and oil are everywhere in complete and accurate contact, that we can expect to obtain good preparations.

The paper case should be sufficiently large to enable the operator to hold it securely. The knife should also be large, as sharp as possible, and on one side at least ground flat. When in use, its upper surface should be wetted with oil of turpentine. On completing the cut, the section should be floated off upon the slide by the aid of a little oil of turpentine. It can then be preserved in the usual way with oil of cloves, Dammar balsam, and a paper cushion.

So far as sections of ova hardened in chromic acid permit us to speak positively in regard to the real form of the parts, the perfectly mature germ has the shape of a biconvex lens, which is somewhat concave at one pole, that, namely, which in the natural position is the inferior. Its diameter amounts to about half a millimeter; its thickness is about 0·05 of a millimeter at the concave, and 0·06 at the biconvex points. In such a sharply defined body the germ has to be sought. The vitelline membrane is above it, and beneath is a finely granulated

mass, of which it cannot at present be stated whether it belongs to the germ or not. Oellacher has not been able to recognize a germ-vesicle in sections made at this stage.

The first groove in the germ was found in an egg that, according to the laying-time of the hen, had remained for twelve or fourteen hours in the oviduct. The body appearing to be the germ was in the already described position, but was somewhat larger and thicker, a sinuous indication of fission of its substance extended somewhat obliquely downwards from the centre of its convex surface.

The second groove was obtained from an ovum, the shell of which already presented some traces of calcification. And again, at the point at which the germ was to be sought, there was a somewhat concavo-convex disk, which however appeared to be thinner and larger than that of the earlier stage. Proceeding from the surface, five clefts penetrated into the interior, splitting the disk into six areas on section. The two most external areas were the longest, but the four middle ones did not materially differ from each other.

In this specimen it was impossible to state with certainty whether there were other, though less defined, morphological elements of the germ *beneath* the above areas.

The next stage was taken from an egg, the shell of which was already consolidated, but was relatively very thin. The germ was here sharply separated from the yolk, and there was a distinctly perceptible cavity between the two. Sections through the centre showed that the germ was composed of polygonal areas, of which six could be counted between the surface and the cavity.

The whole germ, and this term could now be applied with precision on account of the sharp definition of the mass below, always presented an approximation to the form of a biconvex lens, the upper surface of which was adherent to the vitelline membrane, but the under surface of which was irregularly bounded by the flat cavity existing between the germ and the yolk. The marginal areas were the largest, and were filled with larger granules than those more centrally situated. In a few of the areas a nucleus was distinctly visible.

At a subsequent stage, in an ovum also taken from the ovi-

duct, the process of cleavage had progressed to a marked extent. Large polygonal areas were only present at the margin. In the central parts were small granular morphological elements, loosely attached to one another, of which the upper ones were finer, whilst those in the deeper layers were more coarsely granular. In the peripheric parts the germ disk rested upon the yolk, but in the central parts the two were separated from each other by a flat cavity. A few morphological elements, resembling those of the lowermost layer of the germ disk, lay upon the floor of this cavity.

Oviducal eggs of a still later stage presented little more that was worthy of notice. The cleavage had progressed to a somewhat greater extent even at the marginal portions; the morphological elements were in general smaller; the whole disk was somewhat thinner, the cavity somewhat deeper, with a few larger, spherical, strongly granular formed elements resting on its floor. Finally, in one oviducal egg a still more advanced stage of development was met with. The cleavage elements, or embryonal cells, as we may also term them, were partially separable into two laminæ, of which the upper (*S*, fig. 403) was of closer texture, and was composed of smaller cells, whilst the lower (*D*) contained somewhat larger and more coarsely granular cells, so irregularly disposed that in some parts they only formed a single tier, whilst in others they were seen in section to be collected into heaps of from two to three cells deep, presenting in consequence projections at these points.

In freshly laid ova the germ has sometimes undergone no development beyond that which has been already described, whilst in other instances the lower layer, composed of larger cells, is sharply separated from the upper throughout its whole extent.

As a general rule, it may be said that, in freshly laid eggs, the separation of the germ into two layers is sometimes more, sometimes less well marked, but that the cleavage is not as yet quite completed. The morphological elements of the inferior layer are still tolerably large, and some very large cleavage spheroids (*M*, fig. 403) still occur, which project strongly downward towards the cavity, sometimes even touching its floor, so that the blastoderm appears in transverse section to be

supported on pillars. Sometimes such large elements rest upon the floor of the cavity without being in contact with the blastoderm above; in such cases it must remain doubtful whether these elements have been detached during life, or have been separated by the action of reagents. The presence of such variously sized elements lying on the floor of the cavity is however so constant, that it is difficult to avoid the conclusion that they have been separated during life, or have remained adherent to the floor of the cavity when the blastoderm has been raised from it.

Near the free border the blastoderm is thickened, chiefly owing to the large cleavage spheroids situated upon its lower surface, but beyond the thickening the border becomes thin and sharp. It rests with the thickening upon the yolk, and thus lies like a cover over a shallow depression in the latter.

Fig. 403.

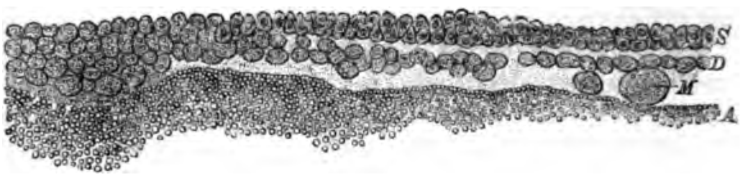

Fig. 403. Section through the germ of a fresh-laid egg in the month of June.

The cavity which is thus formed was termed by Remak the "Germ-cavity" (Keimhöle). The wall bounding the cavity named by His the "Germ-wall" (Keimwall). This wall, however, is by no means a constituent of the germ; it belongs to the yolk, and the term germ-wall is consequently inappropriate.

As the accounts of the layers of the embryo are associated with the last-mentioned stage, this is the place in which a sketch of the literature bearing upon the subject may be introduced.

We are indebted to Caspar Friedrich Wolff* for the prevailing doctrine respecting the development of the Vertebrata from the so-called

* *De formatione intestinorum*, 1768-69. Translated into German by Meckel, 1812.

germinal laminæ. According to his view, the entire composite system of the intestines is developed from a single lamina.

His doctrines were enlarged and completed by Pander.* The blastoderm, he maintains, is composed of a layer of granules, which serves as the rudiment of the future *inferior* germ-layer. A second layer of similar granules develops upon this layer, even during the first hours of incubation, and constitutes the future *superior* layer, so that the blastoderm at the twelfth hour of incubation consists of two laminæ, the upper one of which he named the serous, and the lower the mucous layer. Although he alludes also to the middle layer, under the term "vascular lamina," his description of it is deficient in clearness; for, according to him, it is sometimes an independent structure in which the vessels are developed, but in other instances it is a consequence of the development of the vessels. Nevertheless, he was perfectly aware of the fact that, after twenty-four hours' incubation, three layers, easily separable from one another, are recognizable in the blastoderm. Pander was also the first who endeavoured to sketch out a general plan showing the development of the organism, which he did by referring all the structures and organs that had been termed "animal" from the time of Bichat and Reil to the superior germ-lamina (or epiblast); to these belong the nervous system, with the organs of sense; the muscular and the osseous system. The middle lamina (or mesoblast) he regarded as being simply a vascular lamina; whilst the lower (endoblast) he considered to contain the rudiments of the intestinal system and its associated glands.

The researches of v. Baer † corroborated those of Pander, and may be regarded as a continuation of them; v. Baer described a layer in the non-incubated egg as the first rudiment of a blastoderm; but, in opposition to Pander, he considered that in the course of the first few hours of incubation a second lamina was formed *beneath*, not above, this layer, which constituted the rudiment of the endoblast. The development of the mesoblast (vascular lamina) was described in a manner accordant with the account given by Pander. v. Baer considerably enlarged our views in respect to the general plan of development. He demonstrated the participation of the mesoblast in the formation of the fibrous rudiment of the intestine, as well as in that of the associated glands. He stated that the two layers originating during the first hours of incubation, each divided again into two layers, of which the upper formed the integumental and muscular

* *Loc. cit.*

† *Ueber die Entwickelungsgeschichte der Thiere*, 1822, i.

laminæ; the lower the mucous and intestinal fibrous lamina. The two upper layers he designated the animal; the two lower the vegetative.

Reichert* gave another account. He distinguished in the blastoderm of the fecundated, but non-incubated ovum a layer of corpuscles, from which a membrane (the investing membrane) was developed during the first hours of incubation. The formation of this tunic Reichert regarded as being the first condition for the further development of the embryo, since the yolk cells assumed a laminated arrangement upon its inner surface. The rudiment of the nervous system, he maintained, first makes its appearance, then that of the middle lamina, which, on account of its position between the upper and lower germ layers, he termed the membrana intermedia. After the completion of the formation of this membrane the development of the lower layer commences, the yolk cells depositing themselves upon the lower surface of the former at a time when the embryo begins to be constricted off from the blastoderm. As regards the significance of the blastodermic layers in the further development of the embryo, he considered that the upper lamina takes no part in the formation of the embryo, and that it disappears during the embryonic life of the organism. In regard to the middle lamina, he was the first to show that a division of the lateral plates occurs, and that the middle lamina participates in the formation of the walls of the body. He maintained also that the corneal layer of the integument, the glands of the skin, the muscular, osseous, and vascular systems, as well as the intestinal fibrous layer, with the associated glandular organs, are developed from this lamina. The lower lamina he regarded as representing simply the rudiment from which the epithelium of the digestive organs is developed.

Remak first noticed that the blastoderm of the fertilized but non-incubated egg is composed of two layers. The next changes were referable, according to him, to the inferior layer, which becomes thicker, though it is always looser and less transparent than the upper one. Then follows an histological differentiation of its elements, a layer of cells becoming detached, and covering the inferior surface like an epithelium. As regards the relation of the germ layers to each other in the area of the germinal area (Fruchthof), the upper and middle appear to become thicker, and coalesce at a very early period in the centre of this area. The inferior layer, however, takes no part in this coalescence. With the exception of the middle part of the germinal area, all the three layers may be easily separated from each other throughout their whole extent, both in the vascular area, and in the

* *Loc. cit.*

peripheric parts of the germinal area. Remak endeavoured at the same time with the anatomical independence of the germ layers to establish the relation to the various organs during the further development of the organism. The names that he applied to the laminæ are self-explanatory. The upper lamina, as has been already stated, he termed the corneal or sensorial layer (Hornblatt oder Sinnes blatt); the middle, the motorio-germinal (motorisch-germinatives); and the inferior lamina, lastly, the intestinal-glandular layer (Darmdrüsenblatt), since the epithelium of the intestinal system, with the associated glandular organs, is developed from it.

His,* again, admitted the existence of only a single layer of corpuscles in the fertilized but non-incubated ovum, which constituted the rudiment of the upper germ layer (Archiblast or Neuro-blast). The inferior layer, he considered, develops during the first hours of incubation of the egg by the elongation and junction of the (subgerminal) processes which project from the inferior surface of the upper layer, and consist of one or several rows of cells. The lower layer, on this view, therefore is originally a production of the upper. From these two laminæ the whole embryo, according to him, is formed, with the exception of the blood-vascular system and the group of the connective tissues which develop from the so-called white yolk. In the middle region of the germinal area, moreover, a layer separates from the upper, and one also from the lower lamina; and lastly, an axial connecting band forms between the upper and lower germ layers.

According to Hensen,† the division of the blastoderm into layers occurs at a later period than was admitted by Remak. Hensen also described, as forming at that period of the development of the embryo when the chorda dorsalis has developed in the centre of the germinal area, a "peculiar, consistent, non-nucleated membrane," to which he applied the name "membrana prima." It lies between the epi- and meso-blast, and is more closely adherent to the former than to the latter. He considers it to play an important part in the development of the embryo.

According to Dursy,‡ the centre of the blastoderm (the embryonic shield) consists, at about the fifteenth hour of incubation, of two layers, and the inferior, he believes, may be regarded as the rudiment of the middle germ layer. The statement made by Remak, that the mesoblast is produced by a dilamination of this inferior layer of the blastoderm,

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* *Loc. cit.*

† Virchow's *Archiv*, Band xxx.; Max Schultze's *Archiv*, Band iii.

‡ *Der Primitifstreif des Hühnchens.*

he considers to be not proven. The endoblast is perhaps developed subsequently on the vitelline side.

Waldeyer,* on the other hand, returned again to the view of Remak, that the mesoblast and the intestinal glandular layer proceed from the originally inferior lamina. Waldeyer, however, independently of Peremeschko, recognized that a great part of the cells subsequently existing in the rudiment of the embryo wandered between the blastodermic laminæ. He was not, however, able to decide, so far at least as regards the cells on the floor of the germ cavity, whether they are descendants of the white yolk or are cleavage spheroids.

That which His termed subgerminal processes he did not consider to be a production of the epiblast, but as primary descendants of the egg cells.

I omit the statements of Peremeschko† and Oellacher,‡ as they constitute the basis of the account I here subjoin.

A comparison of my account with the historical review above given, shows that I, like Remak, consider the germ disk of the fresh-laid egg to be composed of two laminæ. I would only add that the division into two is not always complete throughout the whole extent, the laminæ being sometimes still intimately adherent, and the agency of the heat of incubation is required to perfect their separation.

The cells of the lower lamina change their form and arrangement in the course of the first hours of incubation. They become flattened, and appear fusiform on section (*D*, fig. 404). After a few hours, thin sections of well-preserved specimens show with perfect clearness, that two, and only two, layers are present. The upper one is thicker and more compact, and is often composed of two, three, or more tiers of cells; the lower one consists of a number of flattened cells, appearing fusiform on section.

The inferior lamina was indeed, in the first instance, after it had separated from the cloven germ, partially unicellular, though in some parts projecting masses of cells were visible in transverse section. I am unable to state what has in the meanwhile become of these cell masses.

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* *Zeitschrift für rationelle Medicin*, 1869.

† *Wiener Sitzungsberichte*, 1868.

‡ *Loc. cit.*

Peremeschko, however, states that the large granular cells on the floor of the germ cavity augment considerably in number in the course of the first hours of incubation. And, since with this increase in number there is no corresponding diminution in size, it becomes highly probable that the cells projecting downwards from the inferior lamina fall to the bottom of the cavity. This is the more likely, as it is obvious from the appearance above described, that a part of the cleavage elements lying in the lower segment of the germ remain lying upon the floor of the cavity when the germ rises in order to form this cavity.

The lower of the two primary laminæ is, in my opinion, therefore not identical with that which Remak has described under the same designation. According to Remak, the middle and what is subsequently the inferior layer separate from this lower lamina. This, however, is not really an accurate statement of the case. The originally inferior lamina consists, at least before the middle one is formed over the germ cavity, of a layer of flat cells, and it preserves this structure long after the middle lamina is formed. The much thicker middle layer cannot arise by dilamination from this layer of flat cells.

Peremeschko has met with the first traces of the middle lamina at about the seventeenth hour of incubation. The statement of the exact number of hours has only an approximative value, since both the brooding temperature* and the condition of the ovum at the commencement of incubation must be taken into consideration. With this precautionary observation I shall here follow the statements of Peremeschko.

At about the *seventeenth hour* of incubation, then, coarsely granular elements occur here and there between the upper and lower laminæ, which, both in regard to their size and contents, differ essentially from the cells of either of these laminæ, but agree perfectly with those that lie on the floor of the cavity; soon after this the rudiment of the central part of the middle lamina appears. In some preparations it may be observed that

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* I use a water bath for the purpose of incubation, maintained at a tolerably uniform temperature of 39° C. (102° Fahr.) by a self-regulating gas flame.

this rudiment consists already in part of the characteristic cells of the subsequent mesoblast, though in part also of the characteristic coarsely granular large elements (*M*, fig. 404); the upper lamina appears to be tolerably sharply defined from the above-mentioned layer. *The central portion of the mesoblast is thus developed at an earlier period than the rest.* Preparations in which the central part was already developed, exhibited on both sides of it, in the space between the epiblast and endoblast, as far as to the periphery, and somewhat beyond it, new-formed characteristic cells of the mesoblast, in the form of thin layers or small heaps, and sometimes between these, again, the large coarsely granular elements in which the transitional forms from the latter to the heaps of cells may be distinguished. From this observation it must be admitted that the mesoblast is developed from the large coarsely granular elements.

Fig. 404.

Fig. 404. Section of the germ of the Fowl on the first day of incubation.

We thus see that certain morphological elements gradually diminish in number at one point (floor of the germ cavity), where they were previously abundant, whilst quite similar elements make their appearance in an adjoining cavity (between the epiblast and endoblast), and then augment in number, and become converted into collections of smaller cells.

It therefore seems probable that a migration or displacement occurs, by means of which the granulated structures that previously lay upon the floor of the cavity are introduced between the two first germ laminæ.

At about the *twenty-third hour* of incubation all three of the germ laminæ are completely developed. The cells of each lamina possess such characteristic features, that they may easily

be distinguished from each other. A description of the cells of the upper and lower germ laminæ has already been given. Those forming the middle lamina are small round cells with uncommonly delicate outlines and elongated sharply defined nuclei.

As regards the relation of the laminæ amongst themselves, they may be regarded as perfectly distinct, with the exception of the middle part of the blastoderm, where the separation of the middle from the upper lamina cannot be effected.

Peremeschko has examined the variously named large elements lying at the bottom of the cavity on the warmed stage. They change their form at a temperature of from 32° to 34° C. This alteration of form usually consists in a primary contraction and loss of transparency, their form becoming oval or irregularly round; they then begin again to increase in size, and to become more transparent. This alternate contraction and enlargement was several times repeated in one example. The changes in form were observable both in incubated and in non-incubated eggs, but took place with great slowness.

The accuracy of Peremeschko's observations have been corroborated by Oellacher. The perfectly unmistakable appearances presented in similar specimens I have also myself so frequently seen, that I can entertain no doubt of the substantial correctness of his statements.

If we now compare the disposition of the cleavage elements in the germ of Batrachia with that of Fowls, it appears that in Batrachia the external germ lamina, or the sensorial lamina of Remak, is divided into two layers, whilst in the germ of the Fowl it is undivided. In both cases, however, it is developed from a superficial layer of cells which is earlier differentiated than the deeper lamina; from the latter two other laminæ are developed, namely, the inferior and middle laminæ. Thus at a certain stage there exists an opposition common to both between an upper layer of smaller and a lower layer of larger cells.

In Batrachia, as in Fowls, the larger and more slowly dividing cells experience a partial dislocation, passing into a cavity developing coincidently with the process of cleavage. In the Batrachia the large germ cells are attached to the roof of the cleavage cavity, whilst in Fowls the large coarsely granular

elements fall down upon the floor of the cavity, and in order to penetrate between the superior and inferior laminæ must necessarily undergo an active or passive migration.

In both cases the more slowly cleaving large elements form the rudiments of the middle and gland laminæ, and modifications only occur in the mode in which this end is attained. In the case of the Fowl, we know that the middle lamina is not completed with the first rudiment of the embryo. I shall hereafter show that in the course of the second day of development a second migration of large coarsely granular elements occurs for the purpose of forming a rudiment of the vessels, the store of which on the floor of the germ cavity, as I may just state in passing, is not exhausted by the first migration.

In the ova of Batrachia no analogue of the rudiment of the blood-vascular system completing the formation of the mesoblast is discoverable. This, however, may perhaps be referrible to the fact that nothing is at present known in regard to the origin of the bloodvessels in the ova of these animals. In the eggs of Batrachia, also, after the appearance of the rudiment of the mesoblast, a store of large cleavage elements remains behind (fig. 402), respecting the destination of which we know nothing.

(*c.*) GERM OF THE FORELLA (TROUT).—For the purpose of comparison, I shall here briefly give the facts that have been acquired in regard to the embryonal laminæ in osseous Fishes. Rynek* has studied this subject under my inspection in the ova of the Forella, and his are the only researches which give the results of transverse sections. These show that the segmented germ † lies originally in contact throughout its whole extent with the yolk, but that during the expansion of the germ the cavity already known through Lereboullet ‡ is developed. This cavity is completely analogous with the germ cavity of the Fowl's egg. The germ is stretched over the cavity, and rests with a thickened border upon the yolk at the margin of the cavity. The part stretched over the cavity exhibits again, in

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* Max Schultze's *Archiv*, Band v.

† The cleavage was first described by Rusconi in Müller's *Archiv* for the year 1836.

‡ *Nouvelles Recherches et Annales des Science Nat. Zoologie*, Tom. ii., 1864.

its inferior layer, large cells which are disposed, like those of the Fowl, in irregularly distributed heaps. By degrees the inferior surface becomes plane, and the part lying over the cavity then appears to be composed of two layers of uniformly small cells. The upper layer consists of a single tier of cells, but the lower is composed of two or three tiers of cells. Further research showed that the analogue of Remak's sensorial lamina was developed from these two layers. This is here, therefore, as in Batrachia, composed of two distinct rudiments.

Large coarsely granular elements lie on the floor of the germ cavity. The origin of these elements can scarcely be a matter of doubt. The yolk of the egg of the Forella contains no morphological elements from which they can proceed. No other view can be held, therefore, than that they are the remains of the segmented germ which, on the elevation of the latter from the yolk, remain in part lying upon this, and have in part fallen down upon it from above. We thus see the parts around the germ cavity present relations analogous to those we have already met with in the germ of the Fowl.

Fundamental differences, however, do exist, and in order to establish them I must enter into some comparative embryological details. Coste* long ago called attention to the fact that the embryo of the Fish does not originate in the axis of the germ, as occurs in Fowls, but along a part of the thickened border. The relations that are here present may be readily understood by the following conception. Imagine a small sphere of wax placed upon a large wooden ball, and the former flattened out into a disk with a thickened border; the disk continues to expand, its thickened border constantly increasing in size till it reaches the æquator of the wooden ball. And now the wax cap may be conceived to enlarge still further, whilst the thickened border becomes constantly smaller, till when the opposite pole is reached it is reduced to the condition of a scarcely perceptible annulus. The ball will then be almost completely enveloped by the wax cap. Relations exactly resembling the above exist between the germ and the yolk of the egg of the Forella. If the ova at various stages of development be hardened in chromic

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* *Loc. cit.*

acid, and the thick vitelline membrane be cautiously peeled off, the different stages of the process of investment may be followed with the naked eye. Before the cap covers the first third of the yolk sphere, it may be seen that the thickened border is particularly enlarged at one part. With a lens the dorsal groove may here be seen, which is directed towards the superior pole (the original position of the germ).

As the cap enlarges, this rudiment of the embryo increases in size, forming a thickened cord or column of the cap extending from the thickened border towards the upper pole. Finally, when the border is reduced to a slender ring, scarcely visible to the naked eye, it bears a relation to the embryo (the thickened cord) which recalls in a lively manner the relation in which Rusconi's anal aperture of the Batrachian ovum stands to the axis of the dorsal half. Rusconi has himself called attention to this resemblance.

In the Batrachian ovum the dorsal furrow extends from the anal aperture towards the superior pole, though it does not quite reach to it. The thickened cord representing the dorsum of the embryo of the Forella has precisely the same relation to the annular remains of the thickened border which, as is self-evident, bounds a canal. In the egg of the Forella, however, the yolk is exposed by means of this canal, whilst in the Batrachian ovum, in which there is no yolk, large cleavage cells are exposed.

The whole remainder of the cap constitutes to some extent the wall of the body, but is in chief part a yolk sac.* The centre of the germ disk, which has thus been shown originally to lie over the germ cavity, is in Fowls the most important part, being in fact the proper embryo, whilst in Fishes it forms only the rudiment of the yolk sac. In both germs the deep-lying large cells fall upon the floor of the germ cavity. In Fowls, however, a layer remains behind to form the intestinal glandular layer. In the Forella all fall down, and scarcely any glandular lamina is formed in the centre.

If now, at the time when the attenuated centre (S) of the

* See my illustrations in the *Sitzungsberichte der Wiener Akademie*, Band li.

still but little expanded germ lies over the cavity, the larger cells lying on the floor of the cavity be followed towards the periphery, it may be seen that they are directly continuous with the deep layer of large cells which forms the lower layer of the thickened border, and, as it would further appear, the rudiment both of the motorial and intestinal glandular layer.

This relation renders it highly probable that the large cells on the floor of the germ cavity migrate towards the periphery, in order to form or to strengthen the large-celled deposit there found. It is further to be remarked that a rich plexus of blood-vessels develops beneath the walls of the yolk sac, and that the large cells upon the floor of the cavity may fulfil some purpose in the development of this plexus.

Fig. 405.

Fig. 405. Section of the germ of Salmo fario.

(*d.*) MAMMALS.—In regard to the first changes occurring in the germ of Mammals, I have scarcely myself made any observations worthy of notice. In this domain I am therefore only a compiler. And, however valuable the literary material before me may be, I am still unable to make more than a limited use of it; first, because I am unable to give here a history of the controversies by which the first positive facts were established; and secondly, because the Mammalian ovum has scarcely been worked over during the most recent epoch of embryology.

The older statements do not accord well with modern modes of expression, and I have no inclination to reconcile the differences at the desk. I prefer to give a concise account, and at the same time to call attention to the fact that in the history of the development of the Mammalian ovum there is a rich field of inquiry to be worked over.

Bischoff first gave an accurate account of the cleavage of the

Mammalian ovum, and in an historical point of view I must maintain this, though Bischoff* himself ascribes the first knowledge of the process to Karl Ernst v. Baer. Bischoff's description is really the first that stands on a level with our present knowledge. In that description it is clearly stated that the germ (yolk) within its investing membrane, and independently of it, breaks up into smaller morphological elements. Thus the ovum of the Rabbit, he says in his excellent treatise, during the cleavage of the germ (yolk) into progressively smaller spheroids, and surrounded by a thick layer of albumen, passes from the oviduct into the uterus. The duration of its passage through the oviduct, from the concordant testimony of De Graaf, Cruikshank, Coste, Wharton Jones, Barry, and Bischoff, appears to be tolerably constantly two days and a half.

The confidence that Bischoff's illustrations inspire, leads us to believe that the cleavage of the Mammalian ovum is not equally uniform throughout its whole extent. Within the uterus a cavity is developed also in the Mammalian ovum, which gradually increases to such an extent that the cleavage elements compressed at the periphery form a very thin layer enclosing the cavity, or, as it may also be described, constitute the wall of a vesicle. In this condition the little ovum had already been recognized by De Graaf. He described it as a minute vesicle composed of two membranes. The external membrane, as Bischoff has clearly shown, is the germ sheath (Keimhülle), but the internal is the proper germ membrane (Blastoderm, Keimhaut). Bischoff further described a dark mass, consisting of spheroids, attached to the germ vesicle at some point of its interior. These, he says, are spheroids which are obviously identical with the spheroids proceeding from the antecedent cleavage of the germ. They must thus in the process of cleavage remain behind those that form the extremely thin and already very clear and transparent wall of the vesicle. Whether the place where these germ cells accumulate is identical with that at which the germinal vesicle subsequently becomes thickened, we must for the present allow to remain undecided.

At this thickened spot ("germinal elevation," Keimhügel of

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* *Entwickelungsgeschichte des Kanincheneies*, p. 66, 1842.

v. Baer, "embryonic stria," "embryonal spot" of Coste,) Bischoff was again the first to observe the occurrence of a division into two laminæ, and his description of the spot in question corresponds exactly to the relations that we have now, with superior aids to research, ascertained to exist in the ova of Birds, Batrachia and Fish. The cells of the animal layer, in accordance with his description, form a dense membrane, whilst the cells of the vegetative lamina are still distinct, and are very delicate and pale. What signification we are to give to these two laminæ, in the present state of our knowledge, I am unable to determine. A single tolerably clear section from the ovum of a Dog of corresponding age led me to think that the two laminæ, of which the germinal vesicle external to the dorsal rudiment (germ elevation, Keimhügel) is composed, are to be regarded as the analogues of Remak's sensorial and glandular laminæ. It is reserved for the future to give a more definite account, especially in regard to the relations existing at the germ elevation.

I am unable to make any further statement respecting a third vascular lamina occurring between these two, which has been much discussed, and which was admitted by Bischoff. It is, in the first place, doubtful whether this middle lamina is really a vascular lamina, or merely corresponds to Remak's middle germinal lamina. The subject of the development of the middle germinal lamina in Mammals requires a fresh investigation. After the knowledge that has been gained by researches conducted on other classes, I cannot venture to reproduce here any of the opinions generally advanced. So far as this lamina really contains the rudiments of vessels, I shall hereafter have to refer to it again.

(*e.*) MORPHOLOGICAL VALUE OF THE GERMINAL LAMINÆ.—It has already been stated that the external germinal lamina (epiblast) contains the rudiment of the central nervous system, of the nervous constituents of the organs of sense, and of the superficial cellular investment of the animal. It has also been explained why I have designated it the conjoined corneal and nervous lamina. In Batrachia, in which the corneal lamina is separated from the nervous lamina, the relations are extremely

clear. The corneal lamina is uniformly thin throughout its whole extent, except where the sucker of the larva originates. From it also develop the internal cellular lining of the central canal, the external cellular coat of the animal, and the cellular investment of all the glands connected with that coat. I have moreover found that the nervous lamina, even at the earliest period, is thickened in the region where the brain subsequently makes its appearance. Proceeding outwards from this point, it becomes gradually attenuated towards the caudal extremity (yolk plug), and rather quickly in all other directions.

No special thickening exists for the rudiment of the retina, since this, as is well known, is developed from the brain (by a process of eversion). Special thickenings however occur for the olfactory, auditory, and gustatory organs.* I have no remark to make in regard to the rudiment of the tactile organ. I can only point out that the nerve lamina, like the corneal lamina, surrounds the entire periphery, and the relation that exists between the peripheric expansion and the tactile organ still remains, therefore, to be investigated.

Notwithstanding the positive statements of Remak, I cannot consider it to be satisfactorily established that nervous structures can also be developed from the middle germinal lamina. The subject still demands further careful investigation. Observations made upon the tail of the larva of the Frog render it probable that the peripheric nerves proceeding from the axis to the periphery originally project as masses of protoplasm. Wherever, however, such protoplasmic masses occur, they may also develop cellular elements in their course and in their interior. As long as this theoretical consideration is not opposed by precise observations, we cannot regard this important question as settled in the sense held by Remak.

The muscular and connective-tissue substances originate from the middle germinal laminæ. This is so readily seen, that, notwithstanding the authority of those who deny it, I shall not enter into any discussion respecting it. In the first place, the chorda belongs to the connective-tissue substances. The

* See the treatises of Schenk and Török in the *Wiener Sitzungsberichte*, Bande l. and liv.

most simple section, however, shows that the chorda takes up the entire thickness of the middle germinal lamina; being in contact above with the central nervous system, and below with the glandular lamina. The vertebræ are differentiated in a paired manner from those portions of the germinal lamina that bound the chorda laterally; and again, the most elementary sections show that these vertebræ, as Remak long ago demonstrated, undergo subdivision. A portion only of each prævertebra is converted into bone; a part certainly becomes muscle, and it may be presumed that a third part becomes the rudiment of the periosteum.

I have further demonstrated* that at the point where the anterior segment of the cranium subsequently appears, bones and muscles are developed by the formation of boundary or limiting lines in an originally homogeneous material, and no doubt can therefore exist respecting the genesis of the connective-tissue substances.

Reichert, as has already been stated, first recognized the splitting of the middle germinal lamina for the formation of the pleural and peritoneal cavities. There is no great difficulty in demonstrating this fact by the means now adopted for displaying the development of the embryo; namely, by sections.

It may be seen that the lateral portions bounding the vertebræ (lateral laminæ, Seitenplatten, Remak) split just as Remak has stated, and become bilaminated, and that the serous cavities develop between them. The walls of these cavities are thus indubitably formed from the middle germinal lamina. For the rest I must refer to the clear description given by Remak, according to whom the upper of these two laminæ applies itself to the conjoined nervous and horny lamina, and the lower to the glandular lamina, in order to form on the one hand the body wall, and on the other the intestinal tube. In the former case the horny lamina furnishes the external cellular investment and the cellular investment of the superficial glands, but in the latter case the intestinal glandular lamina forms the cellular investment of the cavity of the intestines, as

* Reichert and Dubois-Reymond's *Archiv*, 1864.

well as all the glandular organs that project from the intestine. The relations of the first rudiments of the urino-genital apparatus to the middle germinal layer have already been given by Waldeyer, see vol. ii., p. 192, *et seq.*

DEVELOPMENT OF THE SIMPLE TISSUES IN THE EMBRYO.

In regard to the origin of the cells, little remains to be added to that which has been already stated in vol. i., p. 35, of this Manual. I have, however, devoted much attention to the process of cell division, and have found that it may be observed with tolerable facility in inflamed tissues. It is only requisite to maintain the tissues under observation in conditions that are favourable to their vitality.* The results thus obtained by direct observation are identical with the conclusions that have long been arrived at theoretically. The account formerly given, however, does not appear to be quite accurate. It is not necessary that a cell should assume the form of a finger biscuit before it divides. It divides either with the constant performance of amœboid movements,—the body of the cell, owing to these movements, separating into two masses, united by a thin thread which ultimately ruptures,—or the cell forms a ball-like mass, in which a line of division becomes visible, that sometimes disappears, and then again reappears, and so on, till finally the line becomes defined. In such cases we are led to the conviction that division has really taken place when one or both parts resume their amœboid movements, and finally separate from each other. The cells, however, as a rule, do not part company; they divide, and the cement existing between them alone indicates that the division is complete.

The examination of the process of cell multiplication in inflamed tissues has led to certain modifications of the cell theory. It has demonstrated that cells which have already attained such an age that amœboid movements can no longer be observed in them (fixed connective-tissue corpuscles) may under certain circumstances (as inflammation and its conse-

* Stricker, *Studien.*

quences) again become capable of performing such movements. It has established, further, that this does not apply to old cells. It is found also that the external layers of the cells remain unchanged, and that the central portion alone retracts from the neighbouring parts; so that the cell becomes converted into a vesicle, in the interior of which one or more amœboid cells are contained.

The account of endogenous cell formation given by Brücke (vol. i., p. 35) is in remarkable accordance with these facts, and the whole is completed by the observation of Oser,* that the endogenously formed cells escape through fissures in the maternal sheath.

The development of the epithelia and endothelia, after the full description that has been given of them in this chapter, requires no further consideration.

Rollett has detailed the development of the connective tissues in the second chapter of this work. I need only remark, as the subject is on the *tapis*, that I consider the origin of fibrillar connective tissue from cell processes to be demonstrated; and that, on the other hand, I think the splitting up of a homogeneous matrix into fibrils has not been satisfactorily shown to occur.

Our knowledge of the first traces of the embryonic blood-vessels has reference exclusively to the germ of the Fowl.

C. F. Wolff was long ago aware of the fact that the blood was developed in the form of islands in the germ disk of the Fowl, and Pander went a step further back when he showed that Wolff's blood islands proceeded from smaller dark islands which make their appearance both in the transparent area and in the area opaca. These islands, Pander remarks, elongate, become more slender, communicate with each other by their extremities, and form a reddish plexus with transparent meshes. Baer likewise mentioned Pander's islands, but gave rather a confused account of them, and subsequently Pander's observations fell into oblivion. After the appearance of Remak's works, that author was generally credited with the discovery of these facts; and though he

* *Ibidem*, p. 83.

mistook the secondary for the primary stage, he gave a very intelligible description of it.

Remak regarded the completed blood-vascular plexus as the first trace of the system, and as he saw that the vessels were filled with blood, he explained the appearances presented as follows: Cells, he says, coalesce to form cords and plexuses in such a manner that the peripheral elements of each cord coalesce to form a vascular wall, whilst the central ones become blood corpuscles. As a few years later, by means of the silver method, the cell boundaries could be rendered apparent even in the capillaries, the views of Remak appeared to be perfectly well founded.

Some years ago the island-like rudiments of the blood-vessels were rediscovered by Affanasief,* and I may just mention that the research was conducted under my direction; for Affanasief has since stated that his discoveries were not quite satisfactorily made, in which I am unable to agree with him. M. His also soon afterwards expressed himself in favour of the island-like rudiments, and still more recently E. Klein† has arrived at similar conclusions. Various points which remained doubtful in Affanasief's researches have been satisfactorily explained by these authors; and I now proceed to the description of the earliest stages of development of the bloodvessels with the consciousness of being able to treat the question as being finally settled from a morphological point of view.

If a fresh germ disk be examined at the commencement of the second day of incubation, without any covering glass, with moderately strong powers, isolated cell elements may be perceived in the depths of the tissue, in various stages of development, till they ultimately form large bodies provided with vacuolæ, or, in other words, constitute vesicular structures. In optical transverse section, each of these large vesicles gives the impression of being composed of fusiform cells. As the cell increases to form a vesicle, the nuclei in the wall of the vesicle increase also, project towards the cavity of the

* *Wiener Sitzungsberichte*, 1866, Band liii.

† *Wiener Sitzungsberichte*, 1871, Marz-Heft.

vesicle, and ultimately as many fusiform cells appear to be present as nuclei are seen in optical transverse section. Klein has shown that these cells are constricted off from the inner wall of the vesicles, and falling into the cavity of the vesicle, become blood corpuscles.

The isolated cell elements are also recognizable in sections of hardened specimens, and from these it appears that they must be regarded, for reasons that have already been given, like the cells of the middle lamina, as descendants of the cleavage mass, which however now migrate or wander into it. It further appears that in accordance with their definite position they must be regarded as belonging to the middle germ lamina. Thus we see that from a cleavage spheroid or an embryonal cell a blood-corpuscle-holding vesicle, or, as we may also say, a vessel constructed upon the type of the capillaries, but completely closed, is formed. The wall of the vesicle is composed of protoplasm, the nuclei of which have increased in number, and the cavity then originates, as vacuolæ generally arise.

According to the description given by Klein, blood corpuscles are developed endogenously in the cells, owing to buds protruding from the internal wall of the vesicle, which become constricted at the base, and fall into the cavity of the vesicle. But a second mode of endogenous blood formation also occurs, which is more analogous to the well-known endogenous formation of cells. The central part of a large cell sometimes undergoes conversion into blood corpuscles, so that we have before us a cyst filled with blood corpuscles. Essentially both forms are alike, and in both cases closed and blood-corpuscle-containing vessels originate in single and isolated cells.

The walls of such vesicles give off projections, which are at first solid, but subsequently become hollow. The free extremity of a bud of this kind may again grow out to form a vesicle of one form or the other, so that two cysts communicate with one another, or the buds of different vesicles may intercommunicate, or a bud may open into a vesicle, or the vesicles may open directly into each other, and thus a communicating vascular system originates. The formation of buds still continues after the communicating plexus has been formed. In the tail of the Tadpole, where the new formation of vessels

can be observed as soon as circulation has commenced, the formation of buds is so obvious that it cannot be overlooked by any careful observer.

The vascular walls send out processes which augment in thickness, and unite with the processes of other vessels, or with other vessels directly; as soon as these become hollow the communication is established. It is moreover probable that in the tail of Tadpoles free cells acquire processes, and attach themselves to a vessel in order to play the same part which, in accordance with the above description, is played by the vascular processes. My observation that in the tail of the Tadpole blood-containing fusiform cells, closed at both extremities, occur, has recently been corroborated by J. Arnold. These observations render it probable that even in the tail of the Tadpole an endogenous development of blood corpuscles takes place. It is moreover rendered certain, by researches that have been for some time past conducted in my laboratory, that blood can originate endogenously in the so-called vascularizing inflammatory foci (vascularisirenden Entzundungsheerden) the walls of the cells becoming converted into vascular walls. No other mode of the new formation of vessels has as yet been observed.

Originally all vessels, whether they subsequently form the heart, arteries, or veins, are constructed similarly to the capillaries; that is to say, they have only a single nucleated wall, and this wall in the embryonic condition is composed of embryonic cell substance or protoplasm. The increased complexity of structure subsequently acquired by the heart, arteries, and veins, is the consequence of a secondary process in the external wall of the original tubular system, of which we have at present no information. The endothelia of the heart, arteries, and veins have thus the same genetic importance and value as the walls of the capillaries.

Inasmuch as a system of brown lines can be brought into view by the action of nitrate of silver, exactly resembling those of completely developed capillaries, and continuous with the brown striæ of cement of the endothelia both of the arteries and of the veins, we must admit that the striæ of cementing substance must have formed subsequently through-

out the whole system. This process is quite in accordance with the general principles of development. Moreover, in the first rudiments of the middle germinal layer no instance is known of cells coalescing to form a cellular structure. In all epithelia, as well as in all endothelia, we see cell division only so occurring that from one cell two or more cells arise; these, however, never separate from one another, but cementing substances form between them, which indicates the discontinuity of the individual cells. The same views must be held in regard to the originally homogeneous protoplasmic tubes. I must once more adduce the example mentioned in the preface, that the vessels originally appear as if made like a cannon tube, but that they subsequently seem as if constructed on the plan of a chimney.

We know very little as to the mode and place of origin of the blood in the embryo after the completion of the first rudiments of the vessels have been laid down. Reichert* maintained that the blood is developed in the liver; but no satisfactory evidence of this has been adduced. Again, the view entertained by Neumann and Bizzozero as to the origin of the blood in the cancellous spaces of bones cannot be held to explain the origin of the blood during the earliest period of development, since such cancellous tissue is only formed at a later period. At present it is not known whether generally, and if so, how soon, the medullary spaces act as centres for the formation of the blood. For the earlier stages of development, lastly, we can scarcely regard the lymphatic glands as sources of the colourless blood corpuscles, since, as Sertoli † has shown, the first traces of these are only formed in embryoes at a later period of development.

Before I proceed to describe the development of *transversely striated muscular tissue*, I must add a few words in regard to its structure, which did not find a place in chapter vi. Transversely striated muscular fibres are fusiform or cylindrical, with blunt or pointed extremities. Their thickness varies to an extraordinary extent, being sometimes even visible

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* *Entwickelungsgeschichte, etc.*

† *Wiener Sitzungsberichte,* Band liv., 1866.

to the naked eye, though they are often very much smaller; in short muscles they are equal in length to the muscle itself, but in long muscles they do not in general exceed four centimeters (about one inch and three-quarters).

Schwann discovered a sheath investing the fibres, which he termed the sarcolemma, and since his time it is customary to say that the sarcolemma is completely filled with the true muscular substance. The sheath cannot be seen in fresh fibres, but it comes into view when they are treated with water or diluted acetic acid, or, in short, with any reagent that exerts no action upon the sheath, but causes the muscular substance to swell. The sheath ultimately ruptures at some point, the muscular substance protrudes, and the ruptured canal of the sheath then comes distinctly into view. In such preparations, especially if the muscle examined be not fresh, but have been dead for about twenty-four hours, we may sometimes succeed in exhibiting considerable portions of the sheath: it then appears as a very thin, extremely transparent, and as seen with our instruments, structureless membrane.

Schwann also discovered the nuclei of the muscular fibres; these are the muscle corpuscles of authors; and from the exact investigation of these, Max Schultze, as is well known, was led to make the first steps towards the reform of the old doctrines regarding cells.

The muscle corpuscles lie for the most part on the surface of the muscular substance between this and the sarcolemma. Donders* found that in the muscular fibres of the heart the muscle corpuscles occupied the interior of the fibre. Rollett† has further shown that muscle corpuscles are met with in the interior of the substance of the fibres of the muscles in Amphibia, Fishes, and Birds.

Schwann, lastly, demonstrated the fibrils of muscular tissue, which he described as moniliform threads. He attributed the peculiar appearance on account of which these fibres are termed transversely striated to the regular collocation of the thicker and thinner parts of these fibres. For if such a fibre

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* *Physiologie des Menschen*, German translation by Theile.

† *Wiener Sitzungsberichte*, 1857.

be looked at from the surface, lighter and darker bands of a certain breadth are as a rule seen alternating with one another. These bands or zones, he thought, are caused by the regular juxtaposition of thicker and thinner segments of the fibrils. The muscular fibre was thus, as Valentin stated, a fasciculus of fibrils, and since then it has also been termed a primitive muscular fasciculus (Muskel-primitiv-bündel).

Bowman maintained that the fibrils are not originally present in the fibre, but that they are the product of a process of disintegration. In some instances, he says, the fibres do not split in the longitudinal, but in the transverse direction, in consequence of which disks are formed. If a muscular fibre undergo division in both directions,—that is to say, if the whole length were divided into fibrils, and the whole thickness into disks,—minute particles, the "sarcous elements," would be obtained, of which the muscle is properly composed. Rollett objected to this view, that Bowman only described one kind of material, and had overlooked the connecting substance.

Wharton Jones was the first to mention the alternate succession of two different substances in the longitudinal direction of the fibre; namely, the disks and an intermediate substance.

Dobie maintained that the fibrils themselves consisted of two different substances, and described them as composed of a linear series of alternating bright and dark bodies. Rollett assented to this view. He regarded the muscle-substance of the fibre as composed, in Schwann's sense, of a fasciculus of fibrils, each fibril being segmented by an alternation of two kinds of substances, to one of which, on account of its harder contours, he ascribed a greater refractive power than to the other. The stronger refracting substance he termed the chief substance (Haupt-substanz), the other the intermediate substance (Zwischen-substanz). Taking the fibre as a whole, disks of chief and intermediate substance alternate with each other, the latter corresponding to Bowman's disks. Looking at the fibrils alone, the chief substance corresponded to a sarcous element or a sarcous particle. Rollett might at that time already have been acquainted with Brücke's discovery, to the effect that the doubly refractile property was possessed by the

chief substance alone, but was absent in the intermediate substance.

In regard to the internal arrangement of the fibrils, Rollett accepted the views of Leydig, chiefly resting on the examination of transverse sections of firmly frozen ox hearts, according to which the primitive fasciculus is traversed by a lacunar system. He admitted this in consequence of the configuration of the areas which he obtained from transverse sections. On subjecting the sections to maceration for several days, they were found to present the transverse sections of the fibrils. Cohnheim* subsequently examined muscular fibres methodically by the freezing method, and showed that the transverse sections of such fibres may be regarded as transverse sections through the living tissues. From such sections he has found the proper muscular substance to be composed of two quite different substances, one of which is of great transparency, and possesses a strong lustre, whilst the other is less transparent, and has a dull appearance, the relative quantity of the two being unequal. The highly refractile substance he describes as forming a dense trellis-work of slender lines, becoming wider at certain points only, and decussating at all angles; the dull substance, on the contrary, being arranged in the form of a mosaic, with innumerable triangles, quadrangles, and pentagons, separated from one another by the slender bands of more transparent substance. At certain points the particles of the mosaic are separated to a greater distance from each other than elsewhere, owing to the accumulation of the refractile substance; in the middle of these spots are the nuclei of the muscle. Cohnheim regarded the dull areas of the mosaic as the sections of the sarcous elements. He further maintained that the transverse section of the living muscular fibre so far corresponded to the longitudinal view, that in it also the sarcous elements make their appearance, surrounded and enclosed by another substance of a different nature. In regard to the consistence of the latter, Cohnheim states, upon the authority of Kühne's researches, that it must be fluid.

From this account an essentially novel view of muscular

* Virchow's *Archiv*, Band xxxiv.

structure was obtained, and it was concluded that sarcous elements, surrounded by a fluid intervening substance, and laminated (as disks) like the layers of bricks in a wall, composed the muscular substance.

Kölliker* has however more recently opposed Cohnheim's description. He maintains that the areas described by Cohnheim are the transverse sections of muscular columns, which he again regards as composed of smaller fasciculi of fibrils. His account therefore coincides with that given by Leydig and Rollett.

From the description given by Kühne (vol. i., p. 202, of this Manual), it appears that his opinion in regard to the internal structure is essentially the same as that which may be easily deduced from the account given by Cohnheim.

Such was the state of our knowledge on this subject till the appearance, nearly coincidently, of the works of Krause and Hensen foreshadowed an essentially different explanation. According to Hensen,† the structure of muscular fibre is somewhat as follows: In the primitive fibre of a quiescent muscle, each transverse stria is divided into two halves by a dark line. This line is the expression of a fine disk (median disk). There is moreover, not simply an alternation of a highly refractile substance, the intermediate substance, but after the first half of the transverse disk there follows a feebly refractile substance, the median disk; then the second half of the transverse disk; and lastly, the intermediate substance.

Krause‡ gives a different explanation. Each fusiform fibre (muskel-spindel), according to him, consists, independently of the sarcolemma, of a very large number of muscular cases or compartments (Muskel-kästchen). Each muscle case contains a muscle prism, composed of anisotropal material, which almost entirely fills the muscle case. The form of the muscle prisms (sarcous elements) is that of a multangular column, transversely truncated above and below, the transverse diameter of which varies, whilst the height of the muscle prisms, like that of the

* See his Manual of Histology, 1867, and the *Zeitschrift für wissenschaftliche Zoologie*, Band xvi.

† *Arbeiten aus dem Kieler physiolojischen Institut*, 1868.

‡ *Zeitschrift für Biologie.*

muscle cases, is nearly constant throughout the whole vertebrate series. Both extremities of the prism are covered by a thin layer of fluid (muscle-case fluid). Between each two muscle cases is a basal membrane, by which the cases are separated from one enother. Each case, however, only possesses a single lateral membrane, investing it annularly, which fuses with the two terminal basal membranes. The muscle cases are arranged in the form of regular disks in the transverse direction of the spindles, which may be called muscular fibres. Each muscle compartment consists of a basal membrane, which appears in profile as a transverse line. Then in the longitudinal view of the muscle spindles there follows one half of a clear transverse band, a dark transverse band, then the half of the succeeding clear transverse band, then again the transverse line formed by the septum, and so on.

The most noticeable difference in the signification which Hensen on the one hand, and Krause on the other, give to the appearances presented, is that Krause regards that as a muscle prism, and consequently as an anisotropal part, which Hensen holds to be intermediate substance, and an isotropal part.

Heppner* has raised objections to the accounts given by Hensen and Krause. In his opinion, the refractile zone (muscle-case fluid of Krause, transverse disk of Hensen) is only the expression of total reflexion which occurs at the line of demarcation between the chief and the intermediate substance. In support of his views he adduces the circumstance that the position of the refractile band, in relation to the limiting layer dividing it (median disk, Hensen—transverse line, Krause), can be altered by changing the position of the mirror, and that in certain positions of the mirror the bands may disappear altogether. He adduces also the appearances presented under polarised light. If the visual field be coloured by a Nicol's prism, both the refractile band and the dull disks constantly appear to be of the same colour. Both Hensen and Krause, however, maintain that only one of the two is anisotropal.

So far as regards the explanation given by Krause and Hensen of the appearances first described by them, I must

* Max Schultze's *Archiv*, Band v.

declare myself in favour of Heppner's views. I do not, however, consider the matter to be finally settled. Since Heppner conducted his researches in my laboratory I have repeatedly and most carefully worked over the subject of the structure of muscular fibres, but have up to the present time arrived at no positive conclusion upon the point in question.

My researches have been made exclusively upon fresh muscular fibres, which have been placed under the covering glass without the addition of any fluid, and compressed more or less gently by the insertion of a layer of cement between the margins of the cover and the slide. I have also not avoided the object which Hensen so strongly charges Heppner in a recent publication as having neglected; but have for the most part used the muscles of Hydrophilus, because, as several distinguished fellow-workers have pointed out, the muscles of this animal are extremely favourable for this purpose.

When examined with Hartnack's lens, No. 15, it may be seen, in cases in which the still living muscular fibres appear transversely striated, that the intermediate substances (in the sense of Rollett) are not homogeneous. It may in fact readily be shown, especially when they are not very slender, that dark granules lie in a clear matrix. In many cases I could only count two granules in the length of a single disk. Their arrangement in the clear matrix also varies: sometimes the whole intermediate substance appears in the form of a finely granular zone of protoplasm; sometimes it is partially free from granules, or these are thinly and irregularly scattered. It has been stated by many observers, that the intermediate substance appears, according to the focussing, sometimes clear, sometimes dark; but, so far as regards the appearances presented with the No. 15 lens, I can state positively that the intermediate substance is always dark, when in perfect focus, at the point where the granulations are situated, whilst it is always clear where there are no granulations, clearer even than the chief substance. The chief substance remains relatively dull at all focuses.

The appearances presented by the muscular fibres of Hydrophilus, so long as they still move actively, are extraordinarily variable. In those which only appear transversely striated, the

chief and the intermediate substances alternate in breadth; the form of the limiting surfaces of the two varies, so that the intermediate substance sometimes exhibits a nodal point, sometimes again an attenuation. The position of the disks, as regards the vertical line, also varies, being sometimes oblique, sometimes plane and vertical. Moreover, each zone does not implicate the whole surface or the whole area of a transverse section: displacements sometimes occur, giving the impression that one half of the fibre has been shifted about half the breadth of a disk, occasioning the limiting line between the chief and intermediate substance to be interrupted or to be angularly curved.

Other fibres appear transversely and longitudinally striated, the longitudinal striation sometimes traversing both substances, and sometimes being limited to the chief substance. Other fibres, again, appear only longitudinally striated; and others, again, neither longitudinally nor transversely striated. There is no doubt that all these conditions are presented by living fibres. The course of a fibre which is neither transversely nor longitudinally striated is rendered extraordinarily distinct, and it may also be clearly seen how such a fibre suddenly entirely or partially acquires transverse striation, and just as quickly loses it again. In order to make this intelligible, I can only refer to the image presented to the eye by a bird's-eye view of a corps of infantry whilst actively engaged in performing evolutions; and as it sometimes marches in more or less deep columns, and appears with transverse bands of variable breadth; sometimes again formed into lines that are disposed vertically to the direction of the columns; and sometimes, lastly, form squares, in which the transverse and longitudinal striation disappear in order to reappear, one or both, the next moment. Such appearances are, it is obvious, most in accordance with the view that muscle consists of small groups of disdiaclasts and a fluid intermediate substance. We must not at the same time forget that there are many considerations opposed to this view.

It appears to me to be important to mention those works that are chiefly occupied with the muscular tissue as it appears in the lowest forms of animals. Perhaps the works bearing

on this subject may answer the questions that arise more decisively than is possible from researches upon Vertebrata and Arthropods. As I have made no personal observations upon the subject, I must base my account upon the latest published researches, those, namely, of Schwalbe,* to which I would also refer all those that are desirous of becoming better acquainted with the present state of our knowledge and with the literature of the subject. I extract from this work the following statements which are of general importance. In the first place, that the lowest animals in which striated muscular fibres are met with are the Cœlenterata. Max Schultze, Brücke, and Virchow have seen distinct transverse striation in the muscular fibres of the swimming disk of Aurelia aurita, and Kölliker in that of Pelagia and Agalmopsis. Further, it is to be remarked that, according to the observations of Schwalbe, in Ophiothrix fragilis (Echinodermata) the muscle cells between the ambulacral plates in the first place possess a sarcolemma, and, secondly, the muscular substance appears doubly striated. Such systems of lines, according to his statement, had already previously been observed by Mettenheimer in the muscles of Arenicola piscatorum and Nereis succinea. The same appearance has also been observed in Mollusks. The circumstance that the fibre cells of the muscles of Nematodes and Hirudineæ are composed of a medullary substance surrounding the nucleus, and of a cortical substance splitting into fibrils, also seems to me to be of importance. This observation was made by G. Wagener in transverse sections of the dried muscular fibres of Aulosdoma nigrescens, and it was corroborated by Schwalbe in the Hirudo medicinalis. These observations seem to me of importance, because they correspond to a certain stage of development of muscle in the Vertebrata. Lastly, I shall adduce the fact that Weissmann† has divided the muscular fibres into muscle cells and primitive fasciculi, which division has been opposed by Wagener.‡ Wagener regarded the fibrils as the primitive elements of the muscular fibres.

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* Schultze's *Archiv*, Band v.

† *Zeitschrift für rationelle Medizin*, 1862 and 1864.

‡ *Archiv von Reichert, etc.*, 1863.

I can now discuss but very briefly the development of the muscular fibres. So far as my observations extend in the embryoes of Rabbits, I must support the views of Remak and those who agree with him, that a muscular fibre proceeds from a cell, which elongates and becomes fusiform, and at the same time increases in thickness; the nucleus then increases, and on its surface appears a mantle of longitudinal striæ, which at the same time represents the cortex of a nucleated and granular medullary substance. As soon as this mantle is formed, fibres may also be met with, in which the transverse striæ are apparent. Up to this period it appears as if each fusiform cell were undergoing gradual conversion into muscular substance from the periphery towards the centre. It is important to notice that the first traces of muscular substance in the fibre cells constantly appear to be fibrillar. It must, however, also be stated that it is impossible to investigate such fibres in a perfectly fresh condition. When they are removed from the living embryo, they rapidly die, and it is therefore not easy to determine whether the muscular substance is always fibrillar at its first appearance. In regard to the development of the sarcolemma, I must mention that I can discover no reason, from a study of its development, for considering it as a cell membrane. On the contrary, I have made observations which render it very probable that the sarcolemma is to be referred to cells which attach themselves to the muscle cells, and ultimately enclose them. For if a teased-out preparation be prepared from a trunk muscle of the fœtus of a Rabbit at a time when the muscular fibres are still so imperfectly developed that they are either homogeneous, or are composed of cortex and medulla, it will be found that they lie enclosed in clusters of smaller cells. Moreover we find that more or less strongly projecting nucleated cells adhere to various points of the surface of the fibres when isolated. We may see also how the body of such a cell extends beyond the optical longitudinal section of the fibre as a thin extremely transparent marginal stria, which already presents the aspect of a section of the sarcolemma. With regard to the question of what now contributes to form Schwann's sheath; with regard, further, to the fact that the sheath of Schwann and the sarcolemma are sometimes continuous

with each other, it seems probable that the latter also proceeds from cells which apply themselves to the surface of the muscular fibres. It is to be remembered, however, that those muscle corpuscles that are found between the sarcolemma and the proper substance of the muscle proceed genetically from the latter. This view is based, first, upon the fact that the nuclei of young muscular fibres lie in the medulla; secondly, that the cortex of the cells undergoes conversion into muscular substance; and lastly, upon my observations of the relation of embryonal muscle cells to the smaller cells occurring upon their surface. From this point of view the superficial muscle corpuscles of the sarcolemma are perhaps to be regarded as connective-tissue corpuscles. I must also take this opportunity of mentioning that the muscular and connective tissues are to be referred genetically to one and the same origin, and that, consequent on my account of the superficial muscle corpuscles, it must be admitted that they may aid in the regeneration of the muscles.

The researches of Babuchin have furnished the most recent information upon the development of the nervous system.* From his researches it appears† that there is no essential difference in minute structure between the axis-cylinder processes and the other processes of the nerve cells. It can nowhere be better shown than in embryonal cells that the axis-cylinder process does not communicate either with the nucleus or with the nucleolus: The embryonic nerve cells which have already fully developed axis-cylinder processes, possess a remarkably large nucleus, so that at first sight it appears as if it were quite naked, and was applied immediately to the extremity of the axis cylinder, like the head of a knitting-needle to the needle

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* The plan of the editor was to treat this question in connection with the description of the electric organs. Professor Babuchin undertook this article, and repeatedly visited the coasts of the Adriatic with a view of carrying on his investigations. Babuchin, however, has this year found it necessary to travel into Egypt for pursuing this very study. But as the completion of this work could not be postponed till his return, the editor has determined to stop at this point. The results of Babuchin's researches will appear as a special part supplementary to this work.

† *Centralblatt*, 1868.

itself. By careful observation, however, and with good microscopic powers, a thin layer of protoplasm may already be distinguished, which is sharply defined on all sides from the large nucleus, and gives origin to the axis cylinder. The axis cylinder, which at its origin is relatively thick and conical for the most part, becomes attenuated as it passes outwards, without undergoing division, and is directly traceable into a very slender fibril. In this condition it emerges from the cranial cavity of the embryo, and extends to the most remote parts, where it not unfrequently breaks up into a fasciculus of extremely fine fibrils, only clearly visible with Hartnack's No. 15.

APPENDIX.

I.

ON THE STRUCTURE OF THE SYNOVIAL MEMBRANES.

By EDWARD ALBERT.

BICHAT long ago distinguished the synovial membranes from the true serous membranes, and divided them into two classes: (1) The capsules of the tendinous sheaths—synovial capsules; and (2) the synovial membranes of the joints. No alteration has been made in this arrangement since his time by anatomists, and the only subject of inquiry has been whether the epithelial investment of the synovial membrane of the joints also covers the surfaces of the cartilages. The researches of Hüter,* which appeared in 1866, first gave results that appeared to displace the synovial membranes from the position they so long maintained in the scheme of the membranes of the human body.

From the results obtained by the silvering method, Hüter denied the existence of an endothelium, and maintained that the synovial membrane was lined by a special modification of connective tissue, the form of which sometimes resembled an endothelium, sometimes the serous-canal markings of the cornea (epithelioid and keratoid connective tissue). The modification which the method of v. Recklinghausen experienced at the hands of Schweigger-Seidel † has given results opposed to the statements of Hüter, and Schweigger-Seidel has endeavoured to prove the existence of an epithelium from the presence of nuclei which he finds to be regularly arranged upon the surface.

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* Virchow's *Archiv*, Band xxxvi.; and *Klinik der Gelenk-Krankheiten*, 1870.

† *Arbeiten aus der physiologischen Anstatt zu Leipzig*, 1860.

In a provisional communication, Landzert * has strongly supported the view that the markings are due to the presence of an endothelium, and not to a serous-canal system. On the other hand, R. Böhm,† in his inaugural dissertation, has entirely accepted Hüter's view in regard to the appearances brought into view by the action of silver; but adds that from the results of the investigation of fresh objects in salt and water, he believes he has recognised the innermost layer of the synovialis to be composed of a layer of non-nucleated cells.

If a joint be opened and macerated for a few days in a solution of chromic acid (containing one part of the acid to 10,000 or to 5,000 of water) complete cells may be easily brought into view, forming the internal layer of the synovial membrane, and may be rendered still more distinct by staining with carmine. Under these circumstances a continuous layer of roundish or polygonal cells may be observed, which occasionally possess short processes, and of which each contains a distinct granulated rounded or oval nucleus with nucleoli.

The nucleus sometimes occupies almost the whole of the interior of the cell, so that a small margin only represents the remainder of the cell. In other cases the nucleus is central and small, whilst the body of the cell is larger. It can be clearly demonstrated by this method of research that the deeper layer of the synovialis is coated with complete nucleated cells.

In silvered specimens, again, it appears that two layers of markings can be perceived over large tracts of the synovial membrane. The upper layer presents appearances that essentially resemble the contour lines of the cells forming an endothelium, whilst the subjacent layer exhibits the characteristic markings of a vascular plexus of serous canals enclosing rhombic and quadratic meshes. If this account be compared with that given by Hüter, the most noticeable difference appears to be that, according to Hüter,‡ the epithelial markings lie in the same plane with the keratoid (serous canals). If it can be demonstrated from successful preparations that this is

* *Centralblatt für die medicinische Wissenschaften*, 1867, No. 24.

† *Beiträge zur Anatomie und Pathologie der Gelenke*, 1868.

‡ *Loc. cit.*, p. 43.

not the case, one might be easily induced to consider Hüter's view incorrect (Landzert), and to regard the synovial membranes as simple serous membranes. But the more the subject is investigated, the more do we become convinced that the supposition of the superficial irregular (keratoid) markings being imperfectly brought-out endothelial markings is inadmissible. It may be shown that the markings resembling an endothelium occur indeed over the greater part of the synovial membrane, but that there are nevertheless tracts where they never occur, and in regard to these tracts Hüter's description is undoubtedly perfectly accurate. We may also state in general terms where these tracts are situated. If the highest point of the head of a bone be taken, as, for example, that of the humerus, spheroidal cartilage cells are found around the pole, which in adults are separated by wide tracts of intercellular substance, but in children are in such close apposition that the intercellular substance only represents a slender trellis-work between the cells, giving the whole an epithelium-like appearance. As the æquator of the head of the bone is approximated, cells occur which exhibit angular contours and short isolated processes.

Still further down the cartilage cells are stellate, the processes being relatively very long and occasionally branched, and forming anastomoses. On thus proceeding towards the insertion of the capsule, we arrive at a zone where the cartilage cells gradually pass into connective-tissue corpuscles.*

This is the region of the synovial membrane, and we here meet with vessels that partly form arcades, and partly dip more deeply, and enclose the serous canals in their meshes. No superjacent layer of cells, however, can be perceived at this point. It is only still further down, where the synovial membrane extends as a free membrane from the glenoid cavity upon the head of the bone, that superficial endothelial-like markings become visible.

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* The importance of this fact in supplying an explanation of the serous canals has been clearly pointed out by Böhm. In opposition to Böhm, I have only to observe that the presence of stellate cartilage cells is associated with proximity to the insertion of the synovial membrane, and is not in relation with the mechanical relations of the cartilage, as freedom from friction, etc.

In the synovial membrane, however, there is a zone, the zone of attachment, which in one direction is continuous with the cartilage, but in the opposite forms a serous membrane. The question now arises, whether on the other side of that zone, or, to speak more accurately, between the two zones of attachment (since the synovial membrane is extended between two lines of bone), the membrane preserves the character of a serous membrane in the strict sense of the term. It requires to be determined whether the difference is sufficiently well marked to cause a distinction to be made between the synovial and serous membranes.

The differences are as follows: First, it may be seen in the most successful specimens that the trellis-work of the cementing material does not everywhere present such fine and uniformly broad lines as in the serous membranes; and that the size and form of the cells, and the character of their nuclei, vary to a much more remarkable extent than in them. Secondly, villi are as a rule met with in most joints, as well as in many sheaths of tendons. I have even observed them in the joints of new-born children. Hüter has also stated, as a further point of distinction, that the vessels of the synovial membrane are naked. This feature would certainly be of great importance were Hüter's statement quite correct; but it may be shown that where the layer of investing cells covers the layer of serous canals the cells are also continued over the vessels. In the same way it appears to me that the cells in question are to be distinguished from the endothelia essentially by the circumstance that in the Frog, where the endothelia are so highly developed, such cells are not present on the inner side of the joint, but that there are others which in all these characters agree with the epithelioid cells of Mammals.

Böhm, again, has declared that in the true serous membranes the epithelial layer is never extended over fat, where this occurs, as is the case with the synovial membranes; and he has also further stated that the superficial cells cannot be pencilled away. But as regards the first point, it is to be borne in mind that in true serous membranes the endothelial markings do cover the fat cells. I thus maintain, in opposition to Hüter, that the synovial membrane of the articulations possesses two

layers, an investing cellular layer and a serous canal layer (Säftcanälchenschicht); in opposition to Böhm, that the investing cellular layer is nucleated; and, in opposition to Schweigger-Seidel, that the disposition and form of the nuclei in the investing layer corresponds only exceptionally to his drawings.

The relations of the articular membranes are also remarkably different to the articular ligaments, as may be demonstrated in the articulation of the knee, shoulder, and hip. No ligaments have upon the side turned towards the articular cavity, on which we may admit the existence of a synovial membrane, any investment of epithelial cells, but their surface exhibits the same markings that are apparent upon the surface of the tendons, where they lie free in their synovial sheath. The statement that the cavity of the joint is coated throughout by a closed membrane is thus shown to be incorrect.

The synovial membranes are characterised by the extraordinary richness of their serous canals. It may be demonstrated by treatment with gold or chromic acid, though with difficulty, that this layer contains cells or nuclei. The form of the vessels presents many types.

Böhm first maintained that the bloodvessels are directly continuous with the serous canals. In reality, however, it is the spaces that surround the bloodvessels which communicate with the serous canals.

Hüter states he has never been able to see any lymphatics, and that it is only in inflammatory states, in which the tension of the subsynovial lymphatics is increased, that they sometimes make their appearance. Landzert, on the other hand, declares that they can be distinctly brought into view by his method of silvering.

I have myself been unsuccessful in accomplishing this. In one instance only, in the knee-joint of a Pig, I found distinct lymph cavities running off to a point, invested by an epithelial layer, and lined by an endothelium. Similarly shaped cavities are frequently also to be found in Man; but I have never been successful in finding an endothelium in them. It is possible that some of these were lymphatics; but it is certain that the greater number of these clear spaces are only depres-

sions between folds, into which the solution of silver has never gained access. The folds are rendered uncommonly distinct by the action of the nitrate of silver, and it may be shown that the clear spaces resembling lymphatics correspond to the folds that are visible even to the naked eye.

The synovial sheaths of the tendons—objects well fitted for examination—have the following structure:—The matrix of the duplicatures is composed of fibrillar connective tissue, in which at certain points cartilage cells are constantly present. Superjacent to these are serous canals, similar in arrangement and form to those of the articular membranes. In some parts the framework of the matrix is so slender as to suggest the presence of epithelial structures. More careful observation, however, shows that the relations are here the same as in the zone of attachment of the articular synovial membrane. The structures in question lie upon the same plane as the most distinctly marked ramified structures; and it is not difficult to follow the lines of the matrix widening out and becoming continuous with broad coloured areas. Putting aside the cartilage cells, the lamellæ passing as meso-tendons to the tendons have the same structure as the above.

Finally, the internal wall of the fibrous sheath has the same structure as the surface of the tendon; and in regard to the latter I can only repeat what has been already stated by v. Recklinghausen. The internal wall of the typical mucous sacs or bursæ, a few of which I have examined (in Man), exhibit the same structure, and the same may be said, though from the paucity of the observations, only with probability, of acquired bursæ. As the latter obviously arise from spaces in the connective tissue, we have in the synovial cavities really a transition from simple cavities in the connective tissue to cavities so organised that they stand next to the serous cavities.

II.

ON THE NON-PEDUNCULATED HYDATIDS.

By Dr. ERNST FLEISCHL.

So far as the results of a hitherto incomplete research can be put forward with the plea at least that only facts shall be advanced, the following account may be given.

In the depression between the testis and the head of the epididymis in Man, there is an organ that at its maximum is about equal in size to two peas, but is never wholly absent; it has been recognised by many observers, and has hitherto been described as the "non-pedunculated hydatids of Morgagni." By Krause it has been regarded as the analogue to one of the appendices epiploicæ of the intestine.

This structure, composed of richly nucleated connective tissue, traversed by nerves, bloodvessels, and wide lymphatics, is invested with a layer of ciliated epithelium, which dips into the wide cæcal depressions and involutions of the surface, which are so numerous at the apex of the organ. Running round the base of the organ is a circular, for the most part irregular, line, often perceptible even to the naked eye, which marks the boundary between the "true mucous epithelium" and the flat serous epithelium (endothelium) of the visceral lamina of the tunica vaginalis propria, just as a similar line at the free border of the ostium abdominale tubæ, and that at the base of the ovary, forms the sharply defined line of demarcation between the peritoneum and the germ epithelium. A canal commences near the base of the organ, which, however, I cannot aver to be constantly present, that extends towards the albuginea testis,

and may occasionally penetrate for some distance into its substance.* The walls of this canal are composed of the following layers: Most externally is a cylindrical sheath of densely interwoven, but for the most part circularly disposed, connective-tissue fibres. To this succeeds a thick layer of loose connective tissue, which forms closely arranged folds projecting strongly towards the lumen of the tube, their apices being almost in contact, and having deep depressions between; and internal to this is a layer of columnar epithelium, which is probably also ciliated. The analogy of the whole apparatus with those parts of the female generative organs that develop from the upper layer of the germ-epithelium layer is obvious, and the microscopical aspect of transverse sections of the canal just described, and of the Fallopian tube of the female, bear a close resemblance.

* I have made no mention of this canal in my provisional communication on the "Non-pedunculated Hydatids," (*Centralblatt für die med. Wissenschaften*, 1871, No. 9,) although I was already aware of its existence. Soon after the publication of this communication Herr Prof. Waldeyer was kind enough to forward to me in a letter his views upon the significance of the organ in question, which he had in the meantime examined. This letter contains *inter alia* a complete and excellent description of the canal, and a well-founded suggestion of its nature.

THE END.

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